

JOURNAL

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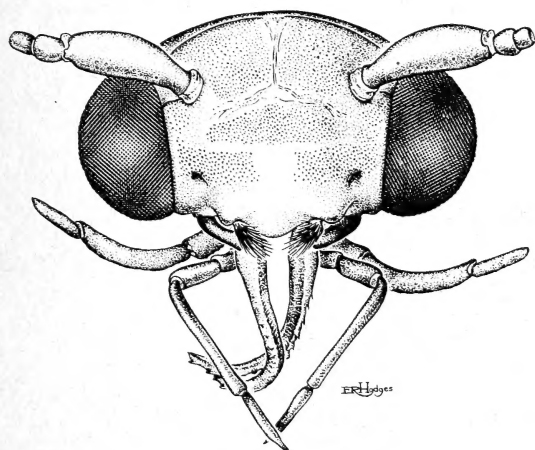
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The object of the Lepidopterists' Society, which was formed in May 1947 and formally constituted in December 1950, is "to promote the science of lepidopterology in all its branches, . . . to issue a periodical and other publications on Lepidoptera, to facilitate the exchange of specimens and ideas by both the professional worker and the amateur in the field; to secure cooperation in all measures" directed towards these aims.

Membership in the Society is open to all persons interested in the study of Lepidoptera. All members receive the *Journal* and the *News of the Lepidopterists' Society*. Institutions may subscribe to the *Journal* but may not become members. Prospective members should send to the Treasurer full dues for the current year, together with their full name, address, and special lepidopterological interests. In alternate years a list of members of the Society is issued, with addresses and special interests. There are four numbers in each volume of the *Journal*, scheduled for February, May, August and November, and six numbers of the *News* each year.

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Cover illustration: The head of a small tineid moth (Tineidae) from Arizona, with all scales removed, illustrating the primitive mouthparts. Original pen and ink drawing by Elaine R. S. Hodges, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560.

JOURNAL OF THE LEPIDOPTERISTS' SOCIETY

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PRESIDENTIAL ADDRESS, 1992: MEGATRENDS AND THE LEPIDOPTERISTS' SOCIETY¹

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With the approach of the 50-year anniversary of the Lepidopterists' Society in 1997, it is appropriate that we begin to think about what type of Society we want for the next half century. I hope that this address will help to identify a few major goals that I believe the Society should pursue.

I joined the Society in 1948, missing charter membership by one year. As a member through its first 45 years, I have a vantage point from which to look back upon our Society and, perhaps, from which to offer some thoughts about its future. It is reassuring to read the premises upon which our Society was founded as stated by Charles L. Remington and Harry K. Clench in the May 1947 issue of the Lepidopterists' News. Three points stand out above the rest: 1) the Society would be devoted to the scientific study of Lepidoptera; 2) its membership would be international; and 3) the Society would include both amateurs and professionals. Harry Clench was able to reaffirm the primacy of these premises twenty-five years later when he wrote the history of the Society in our Commemorative Volume (1945-73). These same principals guide us today, and I hope that they will continue to be central to the Society in the future.

Technological, economic, and political changes are occurring on a vast scale and at a rapid pace. It is never easy to establish policy to accommodate future changes; however, I would like to raise a few

¹ Presidential address presented at the 43rd Annual Meeting of the Lepidopterists' Society, East Lansing, Michigan, 27 June 1992.

TABLE 1. Influence of major trends on the Lepidopterists' Society.

Megatrend	Impact on Lepidopterists' Society
1. Industrial society to informational society	Publication methods
2. High tech/high touch	Butterfly houses Butterfly counts
3. Centralization to de-centralization	Regional lepidopterist societies

questions to our membership, realizing that it probably will require the next five years to evaluate and answer them. I am ever mindful of Mark Twain's famous quip that "predictions are very difficult, especially about the future." My rationale for anticipating the future comes from *Megatrends*, a book written ten years ago by John Naisbitt. Many, but not all, of his predictions have come true. More importantly, Naisbitt provided social and psychological unifying themes to explain major or "megatrends" in the world.

I have chosen three of these themes that have influenced and will continue to influence our Society and the study of Lepidoptera. These are listed in Table 1 with an indication of the type of impact they will have or have had upon our Society.

Industrial Society to Informational Society

Whether the Lepidopterists' Society has made the transition from an industrial to an informational Society may be debated, but new technology undoubtedly has permitted us to transmit and process information more quickly and efficiently than ever before. There are few members left in our Society who received the first issue of the *News* in May 1947. It was mimeographed using a typing stencil. Such stencils now are obsolete and almost unavailable. Everyone who remembers typing on stencils, with their messy correction fluid and their high premium on perfect typing, probably is glad that they have disappeared. Our editor of the *News* now produces camera-ready copy with a computer by a process that wasn't even dreamed of in 1947.

Looking into the future, we should realize that what we see today is but a point on a continuum of change in information processing technology—new approaches are being developed continually. The *Journal of Research on the Lepidoptera* (JRL) now is offering the JRL cumulative index on computer disk. Should we consider something similar? Should we consider the use of compact disks (CDs) not only for indices but also for volumes of the *Journal*? Is our material copyrighted so that the Society could benefit from such a medium? A modest way to begin

computerization may be to advertize in the News for volunteers to assist Richard Arnold with the compilation and data entry for a cumulative "Season Summary." Should we begin to develop regional data bases on Lepidoptera or at least coordinate the standardization of such data bases? Scott Miller strongly suggested this possibility last year in his talk at Tucson. Should we develop a standardized computer format for articles for the News and/or Journal? If the Society plans to make educational materials available to schools, should the material be supplied in machine readable format? Many secondary school libraries now have computer data bases search capability.

High Tech/High Touch

The second theme, high tech/high touch, involves the connection between growth of high technology industries, with their mechanization and impersonalization, and growth of industries that emphasize personal awareness, person-to-person contact, and personal involvement. I believe that this theme is manifested in the growing popularity of butterfly houses. People hear much about the cause and effect behind environmental issues such as ozone depletion, global warming, and pollution. They can achieve some temporary relief from the chaos and experience a little bit of the "Garden of Eden" when they walk through a butterfly house. This same high tech/high touch action-reaction also may explain the increasing popularity of butterfly counts—people want to become involved directly.

How does all this relate to the Lepidopterists' Society? I believe we should take advantage of the growing interest in butterfly houses. We should ask ourselves if we are doing all we can to encourage contributions to our Journal and News for providing the basic background science for mass rearing of Lepidoptera, whether for butterfly houses or potential environmental restoration projects. Terry Domico, a freelance wildlife biologist, recently asked me "for how many of our butterflies and moths do we know enough of the biology that we could undertake a mass-rearing and re-population effort?" He related an interesting story to me in regard to this question. In preparation of a book on the insects of Borneo, he visited Lepidopterists' Society member David Goh at his butterfly farm in Malaysia, where Goh is mass rearing species for butterfly houses. In a few weeks, Domico recorded the life histories of four species of *Troides* that occur in Borneo for which there were no published life history data. This indicates to me that much of the little life history information we have may actually reside, unpublished, in the minds of amateurs. There is a need to get such information into the public domain.

Centralization to De-centralization

The third theme that I have selected from Naisbitt's book is the trend from centralization to de-centralization. Naisbitt relates this trend to changes in government and business practices, and explains it in terms of the growing sophistication and diversity of the populace. For the Lepidopterists' Society, I see this theme exhibited in the proliferation of regional lepidopterist organizations. Currently there are nine of these in the U.S. alone, some more formally structured than others. The growth of these organizations has occurred during a period when membership in our own Lepidopterists' Society has remained more or less constant. A significant portion, but by no means all, of the members of these regional groups are also members of the Lepidopterists' Society. We should not view this movement with alarm nor should we attempt to "coordinate" or control it; we should encourage such groups to form. Our Society can only benefit from such a stance. My wife and I have visited five of the nine organizations, several repeatedly. There is great vitality and enthusiasm there, especially evidenced in local meetings and field trips. This is truly the grassroots of our organization.

What I see in these local groups is a greatly under-utilized resource for making significant contributions to the study of Lepidoptera. There are people willing and able to take part in short and long term survey projects. There are local floral and faunal experts. What is needed is a recognition of this resource and creative leadership to channel its energy toward prioritized local projects. Such efforts will be of extreme value if and when conservation projects are initiated by local and other agencies. This need for professional leadership also was expressed last year by Scott Miller.

These regional lepidopterist organizations represent one of the best means to provide the personalized one-on-one encouragement and education for young people aspiring to learn more about the science of lepidopterology. They are an excellent recruiting mechanism for our Society and the profession.

It is not clear how the Society can further the aims of local lepidopterist organizations without encroaching upon their autonomy. Formalizing and expanding our publication of their activities may help. A forum for local group representatives could be provided at the Annual Meeting. Articles in the News could highlight model activities such as local studies or re-population efforts.

In keeping with the international scope of our Society, we should cover activities of organizations similar to ours in other part of the world. Our "News From Europe" editor, Willy De Prins, is exploring



FIG. 1. *Pyrrhopyge hygieia rufipectus* (Godman and Salvin) (Hesperiidae). Upper photo from 35 mm color slide taken in the Rio Napo area of eastern Ecuador by Joseph T. and Suzanne L. Collins ca. 1970. Lower photo from 35 mm slide taken of color monitor display of the digitized version of the butterfly. Digitization was done at 900 dots/inch using 24 bit color.

increased communication links with SEL (*Societas Europaea Lepidopterologica*).

High Technology

As an example of how technology might impact the study of Lepidoptera in the future, I would like to describe briefly the exciting and rapidly advancing field of high resolution digital imaging.

Biology is a visual response discipline, whether one thinks of field observation, type specimens, or microscopic studies. High resolution color photography is the current medium of choice to record visual data. Sometime within the next five to fifteen years, we will have high resolution digital television in our homes. This will mean easy access to a display device, and because the signals are digital, microcomputers will be capable of analyzing them. Images may be transmitted with high fidelity for publication or analysis where phenotypic information is sufficient. More importantly, new types of quantitative phenotype analysis would be possible.

As an introductory example, I would like to present an image created at the National Center for Supercomputing Applications (NCSA) at Champaign-Urbana. Figure 1 is in two parts. The upper part was prepared from a conventional 35 mm color slide taken in 1970 in the Rio Napo area of eastern Ecuador. The lower portion was prepared in two steps. The original slide was digitized at 900 dots/inch (dpi) in 24 bit color (16.8 million different colors). The digital record of the image was then displayed on a special, very flat, high resolution color monitor and photographed with a 35 mm camera. The resulting 35 mm slide and the original slide were then composited by the printer to produce Fig. 1. The high fidelity of the lower image demonstrates the great promise of digital storage and retrieval techniques for archiving color pictorial information. The price one pays for this fidelity is the need for very large memory storage capability (approximately 70 million bytes per image). Reasonable fidelity currently is widely available in 8 bit color (256 colors). When the high resolution or high fidelity color equipment becomes readily available, images can be placed on compact disks (CDs) and distributed like books, i.e., loaned or sold. Even more important is the possibility of using the images for studies never before possible, such as viewing an image as a predator might view it if the spectral response of the predator's eye (color palette) is known.

In conclusion, a wonderful symbiotic relationship exists within our Society between amateurs and professionals. We now see a similar relationship evolving between our Society and regional lepidopterist groups that share our goals. As a Society, we have benefited directly

from technology in our increased publication capabilities and indirectly from technology's tendency to foster antithetical activities such as butterfly houses, butterfly counts, and participation in local survey and conservation projects. We can look forward to our 50th anniversary with great confidence and high expectations.

ACKNOWLEDGMENTS

I thank Joseph T. Collins and his wife Suzanne L. Collins for loaning me the color slide of *Pyrrhopyge hygieia* and Stephen R. Steinhauser for identifying the specimen. Special thanks go to Kenneth A. Bishop of the University of Kansas Department of Chemical and Petroleum Engineering, and Jay Alameda, industrial consultant, National Center for Supercomputing Applications (NCSA), University of Illinois, for their pioneering efforts to digitize the original image and prepare the 35 mm slide from the display of the digitized image. Thanks also go to Ken Blair of Allen Press for insuring the faithful renditions of the two slides forming Fig. 1.

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THE NATURE OF ANT ATTENDANCE AND THE SURVIVAL OF LARVAL *ICARICIA* *ACMON* (LYCAENIDAE)

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ABSTRACT. I examined ant attendance and its importance to larval survivorship in a facultatively myrmecophilous butterfly, *Icaricia acmon* (Westwood and Hewitson) (Lycaenidae), in a population that uses two host plant species, *Eriogonum compositum* Dougl. and *E. strictum* Benth. (Polygonaceae). Third and fourth instar larvae of *I. acmon* were tended by three ant species: *Tapinoma sessile* (Say), *Formica neogagates* Emery, and an unidentified *Formica* species. Third instar larvae were tended less frequently than fourth instar larvae on both plant species, and *T. sessile* was the attendant ant species for a higher proportion of third instar than fourth instar larvae developing on *E. compositum*. Over the duration of the study, all switches of attendant ant species on individual plants were from early *T. sessile* attendance to later *F. neogagates* attendance. An enclosure experiment revealed that ant attendance had no significant effect on larval mortality.

Additional key words: *Tapinoma*, *Formica*, facultative myrmecophily, Washington, *Eriogonum*.

The association of lycaenid larvae with ants (Formicidae) has provided researchers with model systems for studying the costs and benefits of mutualisms. Recent work has focused on both ecological and evolutionary aspects of these mutualisms, including host-parasitoid interactions (Pierce & Mead 1981), oviposition behavior (Atsatt 1981a, Pierce & Elgar 1985), and the evolution of host choice (Atsatt 1981b, Pierce 1985). To understand the evolution of these mutualisms, it is critical to examine the costs and benefits to both partners. Several field studies have documented the importance of ants to the survival of larval lycaenids (Pierce & Mead 1981, Pierce & Easteal 1986, Pierce et al. 1987, Fiedler & Maschwitz 1989b), but few have experimentally addressed this issue in facultative ant-lycaenid associations (but see Pierce & Mead 1981, Pierce & Easteal 1986). This is particularly surprising when one considers that most lycaenid-ant associations are facultative (see Fiedler 1989a for a recent review). Although the mutualisms studied so far provide excellent ecological and evolutionary case studies, it is important to recognize how variability in the intensity of ant-lycaenid associations might affect generalizations about these systems. To broaden our understanding of facultative ant-lycaenid mutualisms, I conducted an ant enclosure experiment to determine the importance of ant attendance and host plant choice to larval demography in a population of *Icaricia acmon* (Westwood and Hewitson) (Polyommata: Polyommataini) in central Washington.

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STUDY SITE AND ORGANISM

The population of *Icaricia acmon lutzi* (dos Passos) that I studied occupies a bench of the Yakima River, 11.2 miles north of Yakima, Washington at 46°47'N, 120°27'W and 375 m elevation. The habitat represents the *Artemisia/Festuca* zone described by Franklin and Dyrness (1973), but has fewer *Artemisia* and more *Eriogonum* (Polygonaceae) species than typical *Artemisia/Festuca* communities. The four commonest *Eriogonum* species were *E. compositum* Dougl., *E. strictum* Benth., *E. microthecum* Nutt., and *E. elatum* Dougl. The climate in this region is arid to semiarid with relatively warm summers and cold winters. The mean annual precipitation in nearby Yakima is 20 cm with only a small amount (2.9 cm) of this falling during June through August. Average temperatures in the Yakima area in July and January are 21.7°C and -2.5°C, respectively (Franklin & Dyrness 1973).

Although populations of *Icaricia acmon* in this area of Washington have been called hybrids with *I. lupini* (Boisduval) (Goodpasture 1973), regional systematists refer to all populations in the state as *I. acmon* (J. P. Pelham pers. comm.). *Icaricia acmon* ranges throughout much of western North America, and has been recorded feeding on *Polygonum* and at least seventeen species of *Eriogonum* (both Polygonaceae) as well as *Lotus*, *Astragalus*, *Lupinus*, and *Melilotus* (all Fabaceae) (Scott 1986). Subspecies *lutzi* ranges from British Columbia south to central Oregon and east to central Colorado (Goodpasture 1973). In Washington, *I. acmon lutzi* specializes on *Eriogonum*, having been recorded from *E. compositum*, *E. pyrolifolium* Hook., *E. sphaerocephalum* Dougl., and *E. strictum*, and has one or two broods, depending on the site (Peterson, unpubl. data). Larvae diapause in the third instar through winter and resume feeding when their host plant leafs out in the spring. Larvae feed on leaves or flowers by chewing holes in the surface of the structures and inserting their heads to mine out the internal tissues. Several ant species tend the third and fourth instar larvae of *I. acmon*, but earlier instars are not tended (Peterson pers. obs.). California populations of *I. acmon* have four instars and larvae have both a honey gland and eversible tentacles, structures associated with myrmecophily (Ballmer & Pratt 1988). Washington populations are similar in these regards (Peterson pers. obs.). It is not known when these structures first appear in development or if pupae of *I. acmon* are tended by ants.

METHODS

I determined host plant species of the study population of *I. acmon* by following ovipositing females and searching for eggs and young larvae. I observed 73 alightings on *Eriogonum compositum* and *E.*

strictum, two of the three commonest *Eriogonum* species at the site. These alightings resulted in 10 ovipositions, with all eggs laid singly. I saw no encounters with other *Eriogonum* species at the site. In addition, I found eggs and larvae only on these two plant species.

To test the effect of ant attendance on larval demography, I selected 24 pairs of *E. compositum* and *E. strictum* in an area approximately 70 m \times 30 m. Each pair was composed of one plant of each species, with individuals in a pair matched for size and occurring within 0.25 m of, but not in contact with, each other. To exclude ants, I encircled half of the pairs with rings of aluminum flashing which I had painted with Fluon® AD 1 (Northern Products, Inc., Woonsocket, RI), a substance which forms a slippery coating on which arthropods cannot get traction. The base of the flashing was buried 1–2 cm below the soil surface and did not disturb the roots of the plants. In addition, because the soil at the study site had excellent drainage, the flashing could not have retained precipitation. Finally, the flashing was placed far enough from the plants to eliminate shading, and thus should have had no impact on plant quality. I left the remaining pairs without an arthropod enclosure as a control. Onto each of the plants, I placed either ova or early instar (first or early second) larvae of *I. acmon*. I placed two individuals on each plant, for a total of 96 individuals (13 ova and 83 larvae). It is unlikely that at such low densities, larvae would cannibalize each other, especially in light of the fact that in numerous rearings at much higher densities, I have seen cannibalism rarely in this species.

From 7 June to 18 September 1986, I conducted midday censuses at approximately weekly intervals; I resumed the censuses from 17 March to 26 April 1987 (19 censuses total: 13 in 1986 and 6 in 1987). During censuses, I noted the number of larvae on each plant and the species and number of attendant ants. Following the onset of the experiment, 35 larvae appeared in addition to those I had placed on the plants. Twenty-nine of these appeared between the onset of the experiment and 6 July, and the remaining six appeared by 6 August. Presumably, these larvae were already on the plants when I started the experiment or were from eggs that I did not see. I left these additional larvae on the plants because it was impossible to tell individual larvae apart. The distribution of these larvae was as follows: 9 larvae on *E. strictum* control plants, 11 on *E. strictum* enclosure plants, 13 on *E. compositum* control plants, and 2 on *E. compositum* enclosure plants. When larvae reached late 4th instar (the final instar), I collected them and raised them in the laboratory to obtain an estimate of the frequency of larval parasitism. On *E. compositum*, all of the larvae that reached late 4th instar did so from 18–26 April 1987. One larva matured by 6 July 1986 on *E. strictum*, but the remainder that reached late 4th instar did so

from 5–26 April 1987. One of the ant-exclosure pairs was destroyed during the experiment, and larvae on these plants were excluded from the analysis of survivorship. To eliminate problems of autocorrelation, I analyzed ant attendance data with *t*-tests of mean per-plant attendance rates. Overall attendance rates were calculated using data from only the eight census dates on which at least one larva was tended. The reason for this is that on the days when no larvae were tended, it is likely that the lack of attendance had more to do with foraging conditions than larval attractiveness. Larvae were tended on 14, 21, 29 June and 6 July 1986 and 5, 12, 18, and 26 April 1987. For analyses of survivorship, I performed G-tests of independence, applying Williams' 2×2 correction (Sokal & Rohlf 1981). Vouchers of *I. acmon* are deposited in lot #1198 in the Cornell University Entomology Collection.

RESULTS

Ant Attendance

Three species of ants tended *I. acmon* larvae during this experiment: *Tapinoma sessile* (Say) (Dolichoderinae), *Formica neogagates* Emery, and an unidentified *Formica* species (both Formicinae). In all instances, only one ant species tended larvae on a single plant at a given time. Third and fourth instar larvae were tended by these ants, but I saw no first or second instar larvae tended during the censuses.

Tapinoma sessile is a small (2.5–3.5 mm long) dolichoderine ant which tended larvae singly or in groups of up to four ants. When disturbed during censuses, these ants ran to the base of the plant, abandoning the larva they were tending. *Formica neogagates* is larger (3.5–4.5 mm long) than *T. sessile*, tended *I. acmon* singly or in pairs, and was a much more aggressive tender than *T. sessile*. When disturbed, they assumed an alarm-defense posture (Wilson 1971) and would bite any object placed near them. The unidentified *Formica* sp. was similar in size and behavior to *F. neogagates*. I did not collect any specimens of this species. Because I saw only two of these ants and because of their similarity to *F. neogagates*, I combined these two species in the analysis of the composition of attendant ants by instar.

I saw no ant attendance from 13 July 1986 through 29 March 1987 (recall there were no censuses from 18 September 1986 to 17 March 1987); during this time larvae were quiescent and fed rarely. Midday soil temperatures were well in excess of 50°C throughout much of the summer and this may have restricted ant activity. On days when I saw ant attendance, third instar larvae were tended less than fourth instar larvae on both host species (Table 1). In addition, the species composition of attendant ants varied with instar on *E. compositum*, with the di-

TABLE 1. The incidence of ant attendance¹ of third and fourth instar *Icaricia acmon* larvae on *Eriogonum compositum* and *E. strictum* on the eight census dates when ants were observed.

Plant species	Mean % tended	SE	N
<i>E. compositum</i> ^a			
3rd instar	43.3	7.0	11
4th instar	88.9	6.5	7
<i>E. strictum</i> ^b			
3rd instar	10.9	9.1	11
4th instar	53.6	15.8	7

¹ To avoid problems with autocorrelation, I determined the percentage of larvae tended on each control plant. Values are the means of these percentages.

^a $t = 2.66$, 16 df, $P < 0.025$.

^b $t = 2.52$, 16 df, $P < 0.025$.

minutive *Tapinoma sessile* tending a greater proportion of third instar than fourth instar larvae (Table 2). On *E. strictum*, the composition of attendant ants varied similarly, but the differences were not statistically significant (Table 2). Most plants of both species had the same attendant species throughout the study. Interestingly, the six plants that had more than one ant species during the experiment all had *Tapinoma sessile* tending larvae early in the study and *Formica neogagates* tending larvae later.

Survivorship

Ants had no statistically significant effect on the survivorship of larvae to late fourth instar on either host species (Table 3). These data include those extra larvae that appeared after the onset of the experiment, and percentages are from data combined for all plants with similar treatments. All disappearances were interpreted as deaths for these measures of survivorship because it is unlikely that larvae leaving the plants in

TABLE 2. The percentage¹ of tended third and fourth instar *Icaricia acmon* larvae on *Eriogonum compositum* and *E. strictum* that were tended by *Tapinoma sessile*. The remainder of the larvae were tended by *Formica*.

Plant species	Mean % tended by <i>Tapinoma</i>	SE	N
<i>E. compositum</i> ^a			
3rd instar	92.9	7.1	11
4th instar	30.6	16.3	7
<i>E. strictum</i> ^b			
3rd instar	75.0	25.0	11
4th instar	40.0	24.5	7

¹ The percentage of overall attendance was determined for each control plant and values are the means of these percentages.

^a $t = 3.69$, 11 df, $P < 0.005$.

^b $t = 0.78$, 5 df, $P > 0.40$.

TABLE 3. Survivorship of *Icaricia acmon* larvae to late 4th instar on ant-excluded and control plants of *Eriogonum compositum* and *E. strictum*.

Plant species	Ant-excluded	Control
<i>E. compositum</i> ^a		
Survived	4	10
Died	22	25
% survival	15.4	28.6
<i>E. strictum</i> ^b		
Survived	15	11
Died	20	20
% survival	45.5	35.5

^a $G_{corr} = 1.46, P > 0.2$
^b $G_{corr} = 0.37, P > 0.5$.

this harsh environment would survive. Only one parasitoid individual, an unidentified braconid, emerged from the larvae I raised in the lab.

DISCUSSION

The pronounced variability in this association over the course of larval development is notable; third instar larvae on both plant species experienced lower overall attendance rates than fourth instar larvae, and the species composition of attendant ants changed with larval development. Although these results may reflect seasonal changes in the absolute and relative abundances of ants, it seems more likely that larger larvae are more attractive to ants. Fiedler (1989b) showed in a lab study that fourth instar larvae of *Lycaena tityrus* (Lycaenidae) are tended more frequently and with greater vigor than third instar larvae and suggested that an increase in the number and size of pore cupola organs was the cause for this increase. In addition to the pore cupola organs, the honey gland has been clearly demonstrated to play an important role in recruiting ants to lycaenid larvae (Fiedler & Maschwitz 1989a), and it is likely that large larvae produce more honeydew than small larvae. Finally, lycaenid larvae produce calls that serve to recruit ants (DeVries 1991a), and it is again likely that larger larvae could produce louder calls. Any or all of these factors could be important in determining the attractiveness of larval *Icaricia acmon*: pore cupola organs are widespread in the Lycaenidae (Henning 1983, Fiedler 1988); *I. acmon* is known to possess a honey gland (Ballmer & Pratt 1988); and in his survey of lycaenids, DeVries (1991a) found larval calling in several members of the Polyommatainae. If large larvae of *Icaricia acmon* are indeed more attractive to ants, the large, aggressive *Formica neogagates* may simply usurp these larvae from the small, docile *Tapinoma sessile*.

In examining the survivorship data, it is important to recognize that in this study and all other similar studies, the effect of ants on larval survivorship may be somewhat obscured because terrestrial predators were excluded along with ants. The only way to remove ants without removing these predators is to locate all ant nests and selectively isolate or remove them from half of the study area. It was impossible to perform this experiment because the nests of both *F. neogagates* and *T. sessile* are difficult to find. Nonetheless, this is the first experiment showing that lycaenid mortality may be the same in the presence and absence of ants and terrestrial predators. Because of the small sample sizes in this experiment, analyses lacked the power to detect small differences in survivorship between the treatment and control. Had the difference in survivorship between the treatment and control been greater than 25%, the analysis would have detected it. This magnitude of difference is comparable to that found by Pierce and Eastal (1986) for tended and untended larvae of *Glaucopsyche lygdamus* (Lycaenidae). Because survivorship of *I. acmon* larvae on *E. strictum* tended to be higher in the absence of ants, I feel that insufficient statistical power cannot explain entirely the apparent absence of a beneficial effect of ant attendance.

It is quite possible that I would have seen an effect of ant attendance on larval survival had I performed this study in a different place or time. DeVries (1991b) pointed out that variation in the abundances of natural enemies could influence whether riordinid and lycaenid larvae benefit from their associations with ants. In addition, host plant quality, ant abundance, and lycaenid abundance could be important in determining overall benefits. Although temporal and spatial variation in benefits has not been examined in lycaenid-ant associations, Cushman and Whitham (1989) found that the benefits enjoyed by membracids from ant attendance varied markedly over a three year study period. It is clear from the high survivorship of larvae in this experiment that predation and parasitism pressures were low throughout the study period. Had I performed the experiment in a year or region of high larval mortality, I may have seen a difference between the treatments.

Finally, the differences in behavior of the two ant species suggest that they may differ in their effectiveness as defenders of larvae. Although the data here cannot address this issue, Bristow (1984) found that the ant species offering the best protection differed between an aphid and a membracid on New York ironweed. It would be interesting to perform a selective ant removal experiment to test whether the large, aggressive *Formica* species are more effective defenders of *I. acmon* larvae than are the smaller *T. sessile*.

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BISTON BETULARIA (GEOMETRIDAE), THE PEPPERED MOTH, IN WIRRAL, ENGLAND: AN EXPERIMENT IN ASSEMBLING

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ABSTRACT. The melanic form of the peppered moth, *Biston betularia* form "carbonaria," has continued to decline in frequency, comprising only 25.8% of a sample of 933 moths trapped on the Wirral peninsula near Liverpool, England, in 1991. The large sample was made possible, in part, by the use of two assembling traps and a mercury vapor trap. The assembling traps held either females of the North American subspecies, *Biston betularia cognataria*, or native British *B. betularia* females, thus allowing a comparison of the relative effectiveness of the two forms in attracting local males. Our results indicate that British *B. betularia* males do not discriminate between the mating pheromones released by the females of the two races.

Additional key words: "carbonaria," "cognataria," pheromone, industrial melanism.

Previous papers by Clarke et al. (1985, 1990) document the fall in frequency of the melanic form of the peppered moth, *Biston betularia* f. "carbonaria," at Caldý Common, West Kirby, on the Wirral peninsula near Liverpool, England, during the years 1959 through 1989. Figure 1 extends the census showing a slight "hiccup" in 1990 with "carbonaria" up from the previous year from 29.5% to 33.1%. The 1990 sample, however, was limited to only 154 moths, including 51 "carbonaria," 6 intermediates (=f. "insularia"), and 97 pale typicals. In 1991 "carbonaria" dropped precipitously to 25.8%, the lowest figure so far recorded.

The continued decline evidently reflects major habitat modification resulting from reduced industrial pollution accompanying the Clean Air Acts begun in the 1960's although it remains unclear what ecological factors are involved. The typical form of the moth, once widely thought to gain protection from predators by its resemblance to gray foliose lichens, is rapidly replacing "carbonaria" as the common form in the virtual absence of such lichens (Clarke et al. 1985, Grant & Howlett 1988). Clarke et al. (1985) also noted a gradual lightening of the trees in the absence of industrial soot, and Grant and Howlett (1988) have

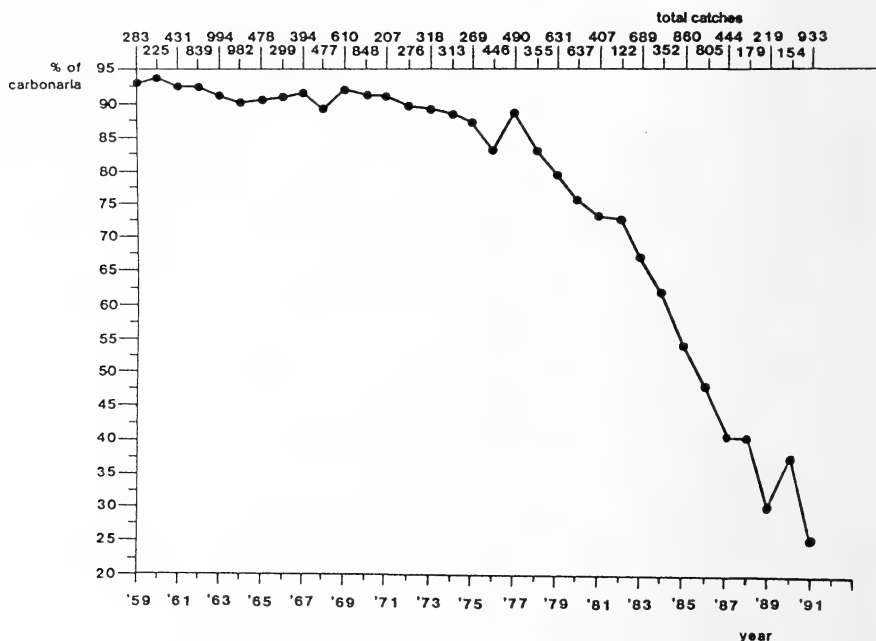


FIG. 1. The decline in the proportion of the melanic form of the peppered moth, *Biston betularia* f. "carbonaria," in West Kirby, Wirral, England. "Carbonaria" is expressed as a percentage of a total in which typicals and "insularia" are combined. The total number of *B. betularia* trapped in the 33 year period was 15,969 of which only 86 were female (0.54%).

further suggested that the comeback of birch trees (*Betula pendula*) following the Clean Air Acts may afford suitable hiding places for both the typicals and the melanics. Atmospheric sulfur dioxide concentrations at West Kirby have dropped markedly during this same period, and with minor fluctuations have remained low in recent years (see fig. 2 in Clarke et al. 1990). The mean winter SO₂ levels (μg per cubic meter) were 20.17 in 1988, 25.25 in 1989, 31.89 in 1990 and the mean for January and February 1991 was 44.39. Whatever the cause, the decline in the frequency of the melanic variant of this species at this location continues.

A second component of our study involved the method of trapping. All 1990 moths were trapped by MV light (mercury vapor lamp) because we had no female *Biston betularia* available that year for use in an assembling trap (AT). The AT is a cage containing virgin females to which local males are attracted by airborne pheromones released by the captive females, i.e., the female odor serves to lure males to the trap. In 1991 we used both MV and AT methods, and we also had the

opportunity of altering the assembling techniques by using virgin female *Biston betularia cognataria* (Guenée) deriving from a large number of pupae brought by one of us (BG) from Virginia, USA.

Biston betularia cognataria is the North American equivalent of *Biston betularia* (L.). It has typical and melanic (f. "swettaria") forms, as well as intermediates grouped together as "insularia" (see West 1977). However, typical *cognataria* generally are darker in appearance than British typicals, and, in fact, have been described as resembling intermediate-grade British "insularia" (see Kettlewell 1973:plate 9.1). Kettlewell (1973) regarded *cognataria* and *betularia* as distinct species because of differences in color and in behavior in the early stages, there often being bivoltinism in the former but never in the latter. Rindge (1975), on the other hand, concluded that the evidence indicates that *cognataria* and *betularia* are members of the same biological species. They can be fully interbred and there is no disturbance of the sex ratio in the hybrids, and both male and female genitalia are identical or nearly so, as is the structure of the male antennae.

We used *cognataria* typicals from Virginia (about 20 at a time in the core of the trap and frequently replenished with fresh females as they emerged) to attract British *B. betularia* males throughout June 1991. Towards the end of this month the *cognataria* emergences were tailing off and the females old. Then our British *B. betularia* virgins (deriving from 20 pupae kindly supplied by Tony Liebert) began to eclose, and we used them in a different trap during July. Our original intention was to produce a quantitative bio-assay of relative pheromone effectiveness, but as we were unsuccessful in coordinating eclosions of the two kinds of females, we were unable to run both assembling traps simultaneously throughout both months. While the period of overlap when both *cognataria* and *betularia* females were available as lures in separate traps extended into July, we must emphasize that the number of individuals present in the cores, and their ages, unfortunately, were not controlled.

Nevertheless, the qualitative evidence that the *cognataria* pheromone is a powerful attractant to *betularia* males is compelling (Table 1). In June, when only *cognataria* females were releasing pheromone from the traps, 329 *betularia* males were drawn in as compared to only 109 males captured by the MV during that same period. During July, when both kinds of females were "calling" simultaneously from separate assembling traps, the numbers of males lured to the traps did not differ significantly by chi-square (144 to the *cognataria*-AT versus 171 to the *betularia*-AT, $\chi^2 = 2.31$, $df = 1$, $0.10 < P < 0.25$). To our knowledge such data on comparative assembling have not been published previously, and, as we have no reason to conclude that the mating pheromones

TABLE 1. *Biston betularia* catches at West Kirby, Wirral, England, 1990 and 1991. Only the MV trap was used in 1990 as no virgin females were available. The 1991 combined catch figures also are subdivided to show numbers taken by each of the three traps used: a) MV trap; b) assembling trap using *betularia* females; c) assembling trap using *cognataria* females.

Year	Trap used	Total catch	Carbonaria	Insularia	Typical	% carbonaria
1990	MV only	154	51	6	97	33.1
1991	All traps combined	933	241	37	655	25.8
1991a	MV trap	289	78	15	196	26.9
1991b	<i>betularia</i> -AT	171	41	4	126	23.9
1991c	<i>cognataria</i> -AT	473	122	18	333	25.8

of *cognataria* and *betularia* are different, our findings are consistent with Rindge's (1975) assessment that *cognataria* and *betularia* are conspecific.

It is true that pheromones occasionally are not entirely species specific, because Clarke (1979) showed that *Orgyia thyellina* Butler (Lymantriidae) females from Japan regularly assembled *Orgyia antiqua* (L.) males in the Wirral, though this is probably an exception to the general rule. The point, however, must be made that Priesner (1975) thought the pheromones of all *Orgyia* species were similar, but the findings were made by antennogram techniques which are not particularly sensitive. If the pheromones in the genus *Orgyia* were alike there would be mating chaos where species fly together, and we know from observation that *O. recens* Hübner and *O. antiqua* do not attract each other (Greenberg et al. 1982).

A final point in the 1991 series relates to the placement of the three traps. Jones, Majerus, and Timmins (unpublished) have produced evidence that in five polymorphic moth species in which melanism is thought to be of ancient origin, great sampling differences in morph frequencies over very short distances occur depending on the local environments in which traps are placed. They suggest that such habitat selection is not likely to be present where the melanism is of recent origin, as in *Biston betularia*, and our 1991 data support this view. Specifically, our MV trap was completely in the open, the *cognataria*-AT under a very thick, old oak tree, and the *betularia*-AT in a relatively exposed position near a small birch tree. Yet, all three morph frequencies were proportionately represented in all three trapping locations. In fact, the three data sets are remarkably homogeneous by G-test ($G = 3.28$, $df = 4$, $0.5 < P < 0.75$).

In summary, the 1991 sample of 933 *Biston betularia* at West Kirby shows a return to the lowering of the proportion of f. "carbonaria," and we report that much of the assembling data resulted from using the American subspecies, *B. b. cognataria*.

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TERRITORIALITY ALONG FLYWAYS AS MATE-LOCATING BEHAVIOR IN MALE *LIMENITIS ARTHEMIS* (NYMPHALIDAE)

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ABSTRACT. A central New York population of *Limenitis arthemis* (Drury) was studied during June and July 1983. Males emerged a week before females with an overall male-biased sex ratio of 1.43:1.00. Of the 30 marked males, 7 (23%) were recaptured within the study area with an average longevity of 10.3 days. No marked female was recaptured. During midday mate-locating behavior, males perched an average of 82.5%, flew for 14.0%, and encountered other individuals for 3.5% of the time. Conspecific males were encountered at a rate of 8.3/h. Conspecific encounters averaged significantly longer than heterospecific encounters (12.8 vs. 5.8 sec). Marked males favored certain areas for perching but changed areas fairly frequently resulting in dynamic territories. Nearly half the perches were on sumac, and 68% were 1-3 m above the ground. Favored territories provided good vantage of female flyways.

Additional key words: activity budget, mark-recapture, protandry.

Territoriality in butterflies is a male tactic to locate receptive females (Powell 1968, Baker 1972, Davies 1978, Lederhouse 1982a, Wickman 1985a,b). Commonly, males defend landscape features such as hilltops and ridges that have high female visitation rates despite their lack of concentrated larval or adult resources (Shields 1968, Lederhouse 1982a, Alcock 1983, 1985, Alcock & O'Neill 1986, Alcock & Gwynne 1988, Rutowski et al. 1989). In addition, areas along butterfly flyways are defended (Baker 1972, Douwes 1975, Bitzer & Shaw 1983). Males of several species defend favorable microhabitats where females may raise their body temperature to facilitate activity (Davies 1978, Knapton 1985). Defense of feeding or oviposition resources appears to be uncommon in butterflies (Baker 1972, Rutowski & Gilchrist 1988, Lederhouse et al. 1992), except where they overlap with emergence sites (Dennis 1982).

Two subspecies of *Limenitis arthemis* (Drury) occur in eastern North America. *Limenitis arthemis astyanax* (Fabr.) is a Batesian mimic of the aposematic, distasteful pipevine swallowtail, *Battus philenor* (L.) (Papilionidae) (Platt et al. 1971, Codella & Lederhouse 1990). North of the geographic range of *B. philenor*, *Limenitis arthemis arthemis* has medial white wing bands. Wing banding is believed to offer protection from predators through disruptive coloration although this has not been demonstrated experimentally (Silberglied et al. 1980). Nearly complete genetic mixing of the two subspecies occurs (Platt & Brower 1968, Platt 1983) except where geographic barriers to gene flow are

present (Waldbauer et al. 1988). In a band between 40° and 45°N latitude, females breed at random with males without regard to degree of male wing banding (Platt 1983).

Males of *Limenitis* species are notoriously aggressive (Pyle 1981, Lederer 1960). Male *Limenitis weidemeyerii* Edwards perch and engage passersby in territorial defense (Rosenberg 1989, Rosenberg & Enquist 1991). Male *L. arthemis* perch in the sun on trees and tall bushes and periodically patrol (Clark 1932, Ebner 1970). Although fidelity of male *L. a. arthemis* (Ebner 1970) and male *L. a. astyanax* (Harris 1972) to particular perches has been noted, Opler and Krizek (1984) stated that male *L. a. astyanax* do not seem faithful to particular sites. This study looked at male mate-locating behavior and population structure of *Limenitis arthemis* in a region of subspecies overlap. In particular, I investigated male longevity, location, aggressiveness, and activity patterns in relation to vegetation structure and local topography.

MATERIALS AND METHODS

The mate-locating behavior of *Limenitis arthemis* was studied near Brooktondale, Tompkins County, New York, during June and July 1983. The study site consisted of a gravel road with hedgerows on each side (Fig. 1). The general area was a mosaic of tilled fields and wooded areas.

Butterflies were captured with a net, marked individually, and released immediately at the site of capture. Redundant marks were placed on both the right and left sides of the dorsal and ventral wing surfaces using red or green felt-tipped pens following a modification of Lederhouse (1978). The identity of a butterfly could be determined at a distance of 3 m or less through observation of a perched or feeding individual. The term "recapture" is used to denote the identification of a marked butterfly either by capture or observation on any day following the date marked.

The presence of *Limenitis arthemis* in the study area was monitored for a minimum of an hour on most sunny days of the study from 1030 to 1630 EDT. New individuals were captured and marked, and marked individuals were identified. The behavior of marked focal individuals was monitored continuously for 15 minute periods. The duration of each activity was recorded to the nearest second and the location noted. All *Limenitis arthemis* activity was recorded for consecutive 15 minute periods in each of three subunits favored by males. The order in which these subunits were observed was determined by random draw. Behavioral observations were conducted during the periods of greatest *Limenitis arthemis* activity (1100 to 1500 EDT).

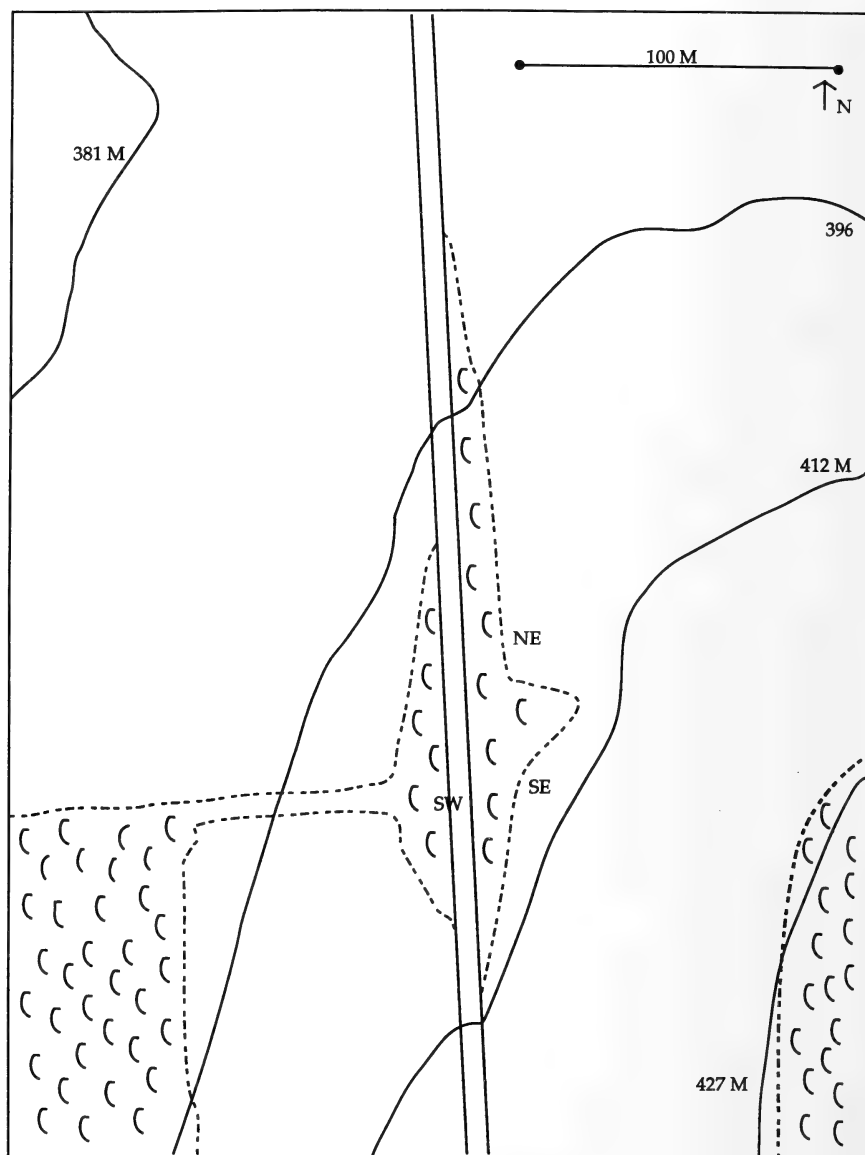


FIG. 1. Map of the Brooktondale, New York, study area.

RESULTS

During the study, 30 males and 21 females were marked. Males first appeared about a week before females; 47% of the males were captured before the first female (Fig. 2). This protandry was significant (Kol-

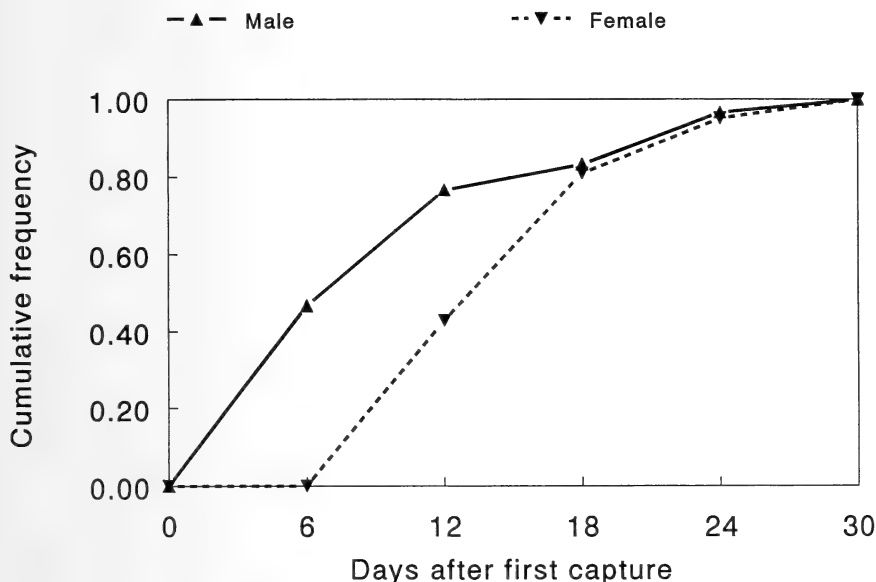


FIG. 2. Cumulative frequencies of male and female captures at the Brooktondale, New York, study area per six day intervals. Day 1 of the generation was 21 June.

mogorov-Smirnov two sample test, $P < 0.01$). Just over 23% of the 30 marked males were recaptured within the study area at least once. Of 7 males recaptured at least once, 71% were recaptured more than once. These 7 males were seen on an average of 4.0 (SE = 0.7) different days. Among multiply recaptured males, the average duration between first and last capture was 10.3 days (SE = 2.0), with three males observed over 17, 16, and 13 day periods. No marked female was recaptured. The overall sex ratio was male-biased (1.43:1.00). Using the method of Manly and Parr (1968) and Manly (1969), the male population was estimated to be 9.3 (SD = 2.0) males for day 7 and 9.0 (SD = 3.0) for day 12 of the study. Only 7% of males and 5% of females had the unbanded *astyanax*-like wing pattern.

Mate-locating behavior by males occurred primarily between 1100 and 1600 EDT. Activity budgets were calculated for a composite male based on 195 min during a total of 11 observation periods of 6 different marked males. Observations were made on sunny days between 1230 and 1500 EDT. The composite male perched 82.5% (SE = 3.8), flew 14.0% (SE = 3.2), and encountered other individuals 3.5% (SE = 0.9) of the time. Encounters with other species occurred at a rate of 1.9 per h; conspecific males were encountered at a rate of 8.3 per h. Hetero-specific encounters were usually brief chases, averaging 5.8 sec (SE =

0.7, $n = 6$). Conspecific encounters were either longer chases or spiral flights and averaged 12.8 sec ($SE = 1.0$, $n = 29$). The difference in duration of conspecific and heterospecific encounters was significant (t -test, $P < 0.01$). Encounters between banded males (13.2 sec, $SE = 1.8$, $n = 10$) did not differ from those between banded and unbanded males (12.5 sec, $SE = 1.2$, $n = 19$).

Most encounters resulted from a perching male engaging another male that flew in the vicinity. The resident male returned from conspecific encounters to the same perch or one within 5 m in 93% of 27 cases. The challenging male returned within a minute after the end of an encounter in 32% of 25 cases. This usually resulted in repeated encounters until only the resident returned. At the study site, territories were linear arrays of perches along the hedgerows. The distance between the two most separate perches for the 11 focal male samples averaged 4.2 m ($SE = 0.6$). Focal males achieved exclusive use of their defended area for 95.1% of the observed period ($n = 195$ min).

Males did not selectively perch on larval hosts. Only 7.7% of 142 perches were on the potential host, black cherry, *Prunus serotina* Ehrh. (Rosaceae). Perches were often on nonhosts staghorn sumac (*Rhus typhina* L.; Anacardiaceae) (48.6%) and white ash (*Fraxinus americana* L.; Oleaceae) (31.0%). The remaining perches were on foliage of non-host trees such as maple and elm, but even raspberry bushes, grape vines, corn, and goldenrod were used. Likelihood of males to perch on sumac during its period of blooming (July 1 to July 10) was not greater than before or after its blooming period (55.0%, $n = 40$, $\chi^2 = 0.9$, $P > 0.3$). Perches were 1–7 m from the ground (Fig. 3) with a mean of 2.9 m ($SE = 0.2$, $n = 142$). The most frequent classes were 2 m (33.8%) and 1 m (21.8%).

Certain locations within the entire study area (Fig. 1) were favored by perching males (Table 1). The southeast (SE) sampling subunit was defended during all but one of the observation periods, and twice as many males were observed in that subunit than in the next most used subunit. Males showed varying site fidelity (Table 1). For 7 males observed on multiple days, a male restricted to a subunit on one day was located in the same subunit on the next day in 62% of 21 possible cases. However, males voluntarily abandoned their territories for short periods. During the observation periods, 27% of 11 focal males were lost when they flew away from the area they had been defending, but were seen in the same areas later the same day.

More females were observed in the SW subunit, which had low male activity. During the study, two unsuccessful courtships were observed. On 27 June at 1318 EDT in the SE unit, a courted fresh female landed on a branch tip with her wings dorsally appressed. The male flew near

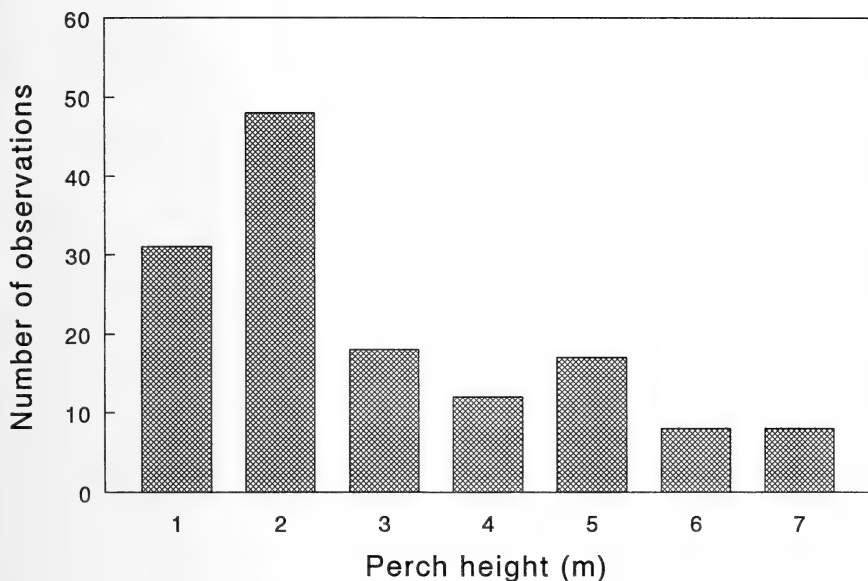


FIG. 3. Distribution of male perches by height in meters. Total sample size is 142 perches.

the female for 10 sec, landed on the same branch, and tried to copulate. The female flew about 1 m and landed on the underside of a leaf with wings dorsally appressed. The male followed the female, landed, and again tried to copulate, but flew off when he was not successful. At 1353 h on 8 July in the NE subunit, another courted fresh female perched on the underside of a leaf, and the male was unsuccessful in his attempts to copulate.

Both males and females fed avidly at the flowers of staghorn sumac. Starting at 1428 h on 1 July, two marked males fed together without aggressive encounters although they were so close that there was some physical contact at the flowers. One female laid an egg on black cherry at 1249 h on 1 July, another laid an egg on apple, *Pyrus malus* L. at

TABLE 1. Male behavior and location of individuals in regard to subunits of the study area. The first two parameters are for 12 0.25-h periods in each area. The last three parameters are for the entire study. Fidelity is the percent of resightings within the same unit. Total females include captures and observations.

	SE	NE	SW
% samples area defended	92	67	50
Total observed males	20	10	7
Initial male captures	11	2	13
% male fidelity to area	82	0	44
Total females	8	1	13

1248 h on 2 July, and another laid two eggs on choke cherry, *Prunus virginiana* L. starting at 1354 h on 5 July. An additional seven eggs and small larvae were found on choke cherry, mostly in the SW subunit.

DISCUSSION

Males of *Limenitis arthemis* defended territories as mate-locating behavior in central New York. Males were localized during midday and early afternoon. Site fidelity from day to day was generally high. Male chases of other males served to secure nearly exclusive use of these sites for the resident male. As in other territorial butterflies (Davies 1978, Rutowski & Gilchrist 1988, Rosenberg & Enquist 1991), the resident generally won these encounters. Conspecific encounters lasted over twice as long as those with other butterflies. The duration of conspecific encounters was quite similar to that for *L. weidemeyerii* (Rosenberg & Enquist 1991), and seems more than adequate to determine the species and sex of the intruder (Scott 1974). Territory turnover was somewhat higher than seen in territorial males of some species (Lederhouse 1982a) but similar to that seen in others (Lederer 1960, Alcock & O'Neill 1986, Rutowski et al. 1989, Lederhouse et al. 1992). Apparently, voluntary abandonment of defended areas was relatively frequent.

The area most regularly defended did not correspond to where most females were observed. The area with the greatest number of females had more trees including more host plants. Five females were observed in oviposition flight in that area. Areas defended by males in this study were independent of larval hosts as in *Limenitis camella* and *L. populi* (Lederer 1960) or adjacent to hosts as in *L. camella*, *L. populi*, and *L. weidemeyerii* (Lederer 1960, Rosenberg 1989, Rosenberg & Enquist 1991). Also, males did not change where they defended during the blooming period of sumac. This suggests that areas most regularly defended are flyways, but not necessarily concentrations of hosts or nectar plants. This is further supported by the preponderance of male perches on nonhosts. Although copulations were not observed during this study, two mating refusal interactions were seen in the early afternoon. Shull (1987) found mating pairs of *L. a. astyanax* at a similar time.

The probability that a marked male would be recaptured was lower than that reported for many territorial species but greater than that reported for patrolling species (Lederhouse 1982b). However, for those males that were recaptured once, the probability of further recaptures was similar to that for other territorial species, as was the number of times those males were seen in the study area. The average residency of territorial males in this study is quite similar to that for the black

swallowtail, *Papilio polyxenes* Fabr. (Papilionidae) from the same area (Lederhouse 1983). The two *astyanax*-like males of *L. a. astyanax* seen in the study area were observed over 16 and 13 day periods, two of the three longest. Central New York is north of the usual range of *Battus philenor* although late season strays are regularly seen there (Shapiro 1974). It is worth further study to determine whether the longevity of these two males was merely coincidental or related to their phenotype.

Although most individuals in this study were banded, their behavior encompassed published accounts for both *L. a. astyanax* and *L. a. arthemis*. Banded and unbanded males clearly recognized each other as competitors for the same territories. Encounter durations between unbanded and banded males did not differ from those between banded males, but both were significantly longer than encounters with other species. This is consistent with the apparent panmixia that occurs where the two subspecies come into contact (Platt & Brower 1968, Platt 1983). Although all females that were observed ovipositing were banded, they laid on hosts usually considered to be hosts of *L. a. astyanax* (Pyle 1981).

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DEVELOPMENTAL CHANGES AND WEAR OF LARVAL MANDIBLES IN *HETEROCAMPA GUTTIVITTA* AND *H. SUBROTATA* (NOTODONTIDAE)

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ABSTRACT. Detailed descriptions and scanning electron micrographs of worn and unworn larval mandibles and physical measurements of cuticle loss owing to wear within each instar were made for *Heterocampa guttivitta* (Walker) and *H. subrotata* (Harvey) (Notodontidae). First instar mandibles of both species lack a retinaculum and are used to skeletonize leaf tissue. The mandibles of later instars have a retinaculum and are more robust. The latter are used to cut through the leaf blade. The retinaculum of *H. subrotata* is bifurcate as opposed to the simple retinaculum of *H. guttivitta*. The teeth and retinaculum on the mandibles of instars two through five of both species are almost completely worn down during their short period of use; the length of mandibles is reduced by at least 20 percent during the final larval instar.

Additional key words: saddled prominent, systematics, morphology.

Mandibular characters of lepidopterous larvae have been used in many taxonomic keys (Gardner 1946a, 1946b, Beck 1960, Godfrey 1972, Brown & Dewhurst 1975) and in phylogenetic studies of various Notodontidae (Godfrey et al. 1989). However, relatively little research has focused on the functional morphology and feeding ecology of lepidopterous larval mandibles (Tragardh 1913, Bernays & Janzen 1988), and no study has accounted for wear of these structures. Thus, the reliability of some mandibular characters may be questionable. The purpose of this study was to document the ontogenetic changes of larval mandibles of *Heterocampa guttivitta* (Walker) and *H. subrotata* (Harvey) (Notodontidae) and to determine the extent of wear on the mandibles within each larval stadium of both species.

Heterocampa guttivitta, the saddled prominent, is an occasional pest in hardwood forests in the northeastern part of the United States. In the past it has caused reduction in yields in the sugar maple and lumber industries. *Heterocampa guttivitta* has five larval instars and overwinters in the pupal stage. In the northeast it has one generation per year, with the moth emerging in May-June (Forbes 1948). In central Illinois there are two generations per year, with the moths emerging May-June and July-August, based on collection records in the Illinois Natural History Survey (G. L. Godfrey pers. comm., Illinois Natural History Survey, Champaign, Illinois). The larvae have been reported feeding on *Acer* (Aceraceae), *Betula* (Betulaceae), *Carya* (Juglandaceae), *Castanea dentata* (Fagaceae), *Corylus* (Corylaceae), *Fagus* (Fagaceae), *Hamamelis virginiana* (Hamamelidaceae), *Juglans* (Juglandaceae), *Malus pumila* (Rosaceae), *Ostrya virginiana* (Corylaceae), *Populus* (Salicaceae), *Prunus* (Rosaceae), *Pyrus* (Rosaceae), *Quercus* (Fagaceae),

Rubus (Rosaceae), *Spiraea* (Rosaceae), *Ulmus* (Ulmaceae), and *Viburnum* (Caprifoliaceae) (Tietz 1972).

Heterocampa subrotata is the smallest *Heterocampa* species in North America. The "evenly green form" or variety "celtiphaga" (Forbes 1948) was used in this study. Larval hosts have been reported as *Acer*, *Betula*, *Carya*, *Cornus* (Cornaceae) and *Hamamelis virginiana* (Teitz 1972). *Heterocampa subrotata* also has five larval instars and overwinters as a pupa. It appears to have two generations in central Illinois, with adults emerging in May-June and July-August.

METHODS AND TECHNIQUES

Collecting and Rearing

To ascertain the feeding histories of the larvae used in this study, larvae were reared from eggs deposited by wild females. Three *Heterocampa guttivitta* and five *H. subrotata* females were collected at a UV-light trap in Trelease Woods, Champaign County, Illinois. One *H. guttivitta* was collected at a similar UV-light trap in Wolf Creek State Park, Shelby County, Illinois. All life stages of both *Heterocampa* species were maintained in an insectary and were exposed to ambient temperature and humidity during the summer of 1989 in Champaign, Illinois.

Voucher specimens of both study species are placed in the Illinois Natural History Survey Insect Collection, Champaign, Illinois. Voucher specimens include the pinned adult females from which eggs were obtained, as well as alcoholic specimens of the following: eggs just prior to hatch, intact larvae from each stadium, and head capsules from the exuviae of all five larval stadia. George L. Godfrey verified all species identifications.

Individual field-collected females were placed into one-ounce plastic diet cups with cardboard lids. Each cup contained a strip of brown paper towel which served as a resting spot for the moth and as a possible oviposition site.

Four cohorts of *Heterocampa guttivitta* and five cohorts of *H. subrotata* were reared. Each cohort consisted of approximately 45 individuals. To reduce mortality attributable to handling, fresh leaves and the diet cup containing unhatched eggs were placed into a rearing container. Rearing containers were plastic Solo (P550) cups with a depth of 5 cm, a top diameter of 8 cm, and a bottom diameter of 5 cm. The cups were fitted with clear plastic lids. Newly hatched first instar larvae were allowed to crawl onto the leaves. After one or two days of feeding, the leaves were cut so that each section had only one larva on it. Each leaf section with a single larva was placed in a separate rearing container with additional leaves. The addition of several leaves to a container

helped minimize the loss of leaf moisture. The larvae were reared individually in the described containers until reaching the prepupal stage.

An unknown percentage of larvae of both *Heterocampa* species in this study were infected with a cytoplasmic polyhedrosis virus (CPV) (J. V. Maddox pers. comm., Illinois Natural History Survey). Individuals in six of the eight cohorts reared for this study displayed symptoms consistent with those typical of CPV infections.

The CPV infection did not produce a high mortality in the larval cultures and was not diagnosed until most of the larvae had reached late third instar. Larvae were discarded and not used in this study if they displayed any symptoms consistent with a CPV infection. No attempt was made to histologically determine if larvae used were infected with CPV. The assumption was made that a CPV infection that produced no physically visible symptoms would have little or no effect on mandibular morphology or on the general nature of how mandibles wear with use.

Heterocampa guttivitta was reared on white oak (*Quercus alba* L., Fagaceae) and *Heterocampa subrotata* was reared on northern hackberry (*Celtis occidentalis* L., Ulmaceae). White oak foliage was replaced every third day or earlier if the existing foliage appeared to be dry. Northern hackberry was replaced every day or every other day depending on foliage condition. Dark green, mature leaves of northern hackberry and white oak were collected fresh each morning.

Prepupae were placed in half-pint cardboard ice cream containers (with no more than three individuals of the same species per container) that contained an approximately 2-cm layer of sand covered with approximately 4 cm of moist peat moss. Larval exuviae were carefully removed from the pupal chambers and stored in 70-percent ethanol until the mandibles could be dissected from the head capsule and measured.

Unworn mandibles were collected from newly molted larvae. It was difficult to obtain larvae that had not fed unless they were isolated from the foliage before ecdysis. This was done by carefully cutting a small section from the leaf that contained the silk mat and larva. The leaf section, silk mat, and any remaining exuvia were removed after the larva had completed molting and begun moving around the container. Larvae were not used if they had fed on the dry leaf sections after molting. However, a majority of the larvae did eat part of their exuviae. The assumption was made in this study that feeding on exuvia caused negligible wear; no effort was made to keep the larvae from feeding on it or to determine if any wear was produced by this type of feeding.

Newly molted larvae were held without foliage for 8–12 hours before

being preserved. Mandibles that were not allowed to harden in this manner were difficult to dissect without tearing or otherwise damaging them. Larvae were killed in boiling water and subsequently preserved in 70-percent ethanol until the head capsules could be measured and the mandibles dissected and measured. Both the left and right mandibles were removed from intact, preserved larvae as described by Godfrey (1972). If the mandibles were not completely sclerotized at the time of preservation, the abductor muscle was cut where it attached to the mandible, but the adductor muscle was removed with the mandible. Excess muscle tissue was removed before the mandibles were measured.

Mandibles from exuviae were used to represent the worn condition because they could be obtained in a non-destructive manner, and because they potentially demonstrate maximum wear. Head capsules were collected from the rearing containers with a small camel's-hair paint brush and placed directly into 70-percent ethanol until they could be measured and the mandibles could be removed and measured. Mandibles were removed from molted head capsules by severing any cuticular attachments and lifting out the mandibles with a curved dissecting tool. They were returned to 70-percent ethanol after being measured.

Scanning Electron Microscopy Preparation

Mandibles were washed in three changes of 70-percent ethanol and then sonicated in a 1:1 solution of Photo-Flo and 70-percent ethanol for 30 seconds. Seventy-percent ethanol was used in the sonicating fluid to keep the mandibles from floating or sticking to the sides of the container above the fluid line during sonication. Sonication times of over 30 seconds occasionally result in lost or damaged setae. After sonication, the mandibles were washed three to five times in 70-percent ethanol and were then dehydrated in a graded ethanol series: 85%, 95%, and three times in 100% (10 minutes in each concentration). The specimens were critical-point dried and attached to stubs using aluminum tape. The tape worked very well for attaching the small samples, which had a tendency to sink into liquid adhesives. However, aluminum tape produces a light-colored background, which may interfere with the viewing and photographing of the specimen. The specimens were coated three times with gold-palladium. Each coating was for 30 seconds at 30 mA. An AMRAY 1830 scanning electron microscope operating at 10 kV was used to view the specimens.

Statistical Analysis

Six to fifteen randomly chosen pairs of mandibles from each species, representing each stage of development (1st to 5th instar) and both

states of wear (unworn and worn) were measured in order to determine the extent of wear. Two measurements were taken of each mandible: the distance between the condyle and the adductor apodeme (CI) and the distance from the condyle to the tip of the second tooth (CT) (Figs. 1-2). Teeth were not discernible on worn mandibles from stadia three, four, and five. In those cases, the point most distad from a line connecting the condyle and the adductor apodeme was used in place of the second tooth (Figs. 1-2). CT and CI were taken for both right (R) and left (L) mandibles to produce four groups of measurements (RCT, LCT, RCI, and LCI) for each pair of mandibles. CI measurements were taken to ensure that changes in the length of the mandible (CT) were due to wear and not due to changes that resulted from sclerotization.

All measurements were taken at the highest practical magnification for each group (e.g., all first instar RCI and LCI for *H. subrotata* were taken at 120 \times) through a dissecting stereomicroscope with an ocular micrometer that had been calibrated with a stage micrometer.

Means and standard deviations for RCI, LCI, RCT, and LCT were calculated for each state of wear in each instar. An unpaired *t*-test was used to test for differences between means of unworn and worn mandibles. A paired *t*-test was used to test for differences between right and left mandibles from the same larva.

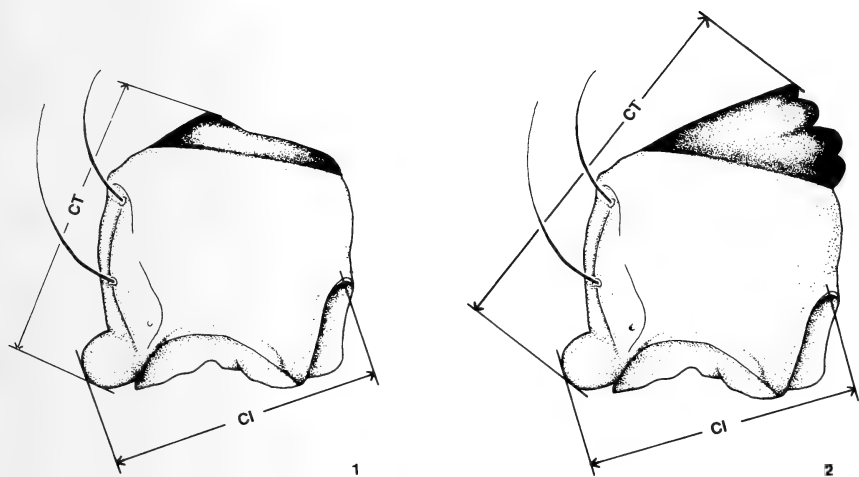
RESULTS

Mandible Descriptions

Notodontid mandibles are hollow structures with the distal (cutting) edge heavily sclerotized. They appear dark caramel brown in color under a dissecting stereomicroscope. The proximal end is open. There are two points of articulation on the mandible (Figs. 3-5). The condyle (C) articulates with the subgena and the acetabulum (A) (=socket) articulates with the lateral part of the clypeus.

There are four surfaces on the mandible: lateral, dorsal, ventral, and oral. These surfaces are defined with respect to the orientation of the mandible to the caterpillar. There is a textured area on the lateral surface, which is located in a slight depression. Two setae (M1 and M2) (Beck 1960) can be found in this area (Figs. 4-5).

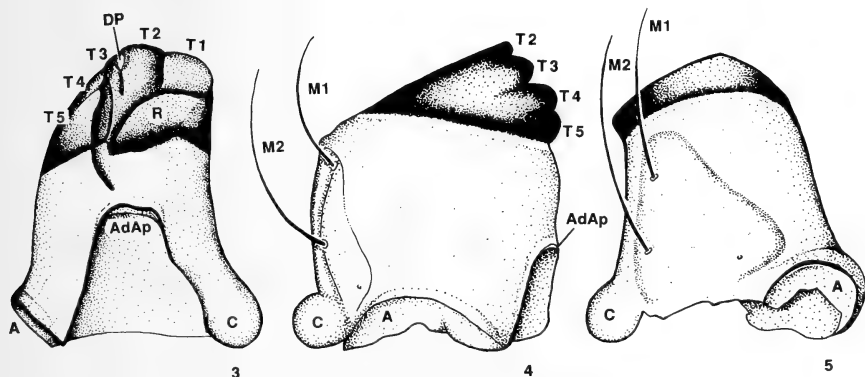
The oral (=inner or mesal) surface was the emphasis of this study. Leaf cutting occurs on the extreme distal edge of the mandible. This edge may be smooth or it may have a series of teeth (dentes). The teeth are numbered from the ventral to the dorsal surface with Arabic numerals (Fig. 3) (Godfrey 1972). A retinaculum (R) or inner ridge is usually present in notodontids (Fig. 3). The retinaculum is part of the heavily sclerotized distal end of the mandible.



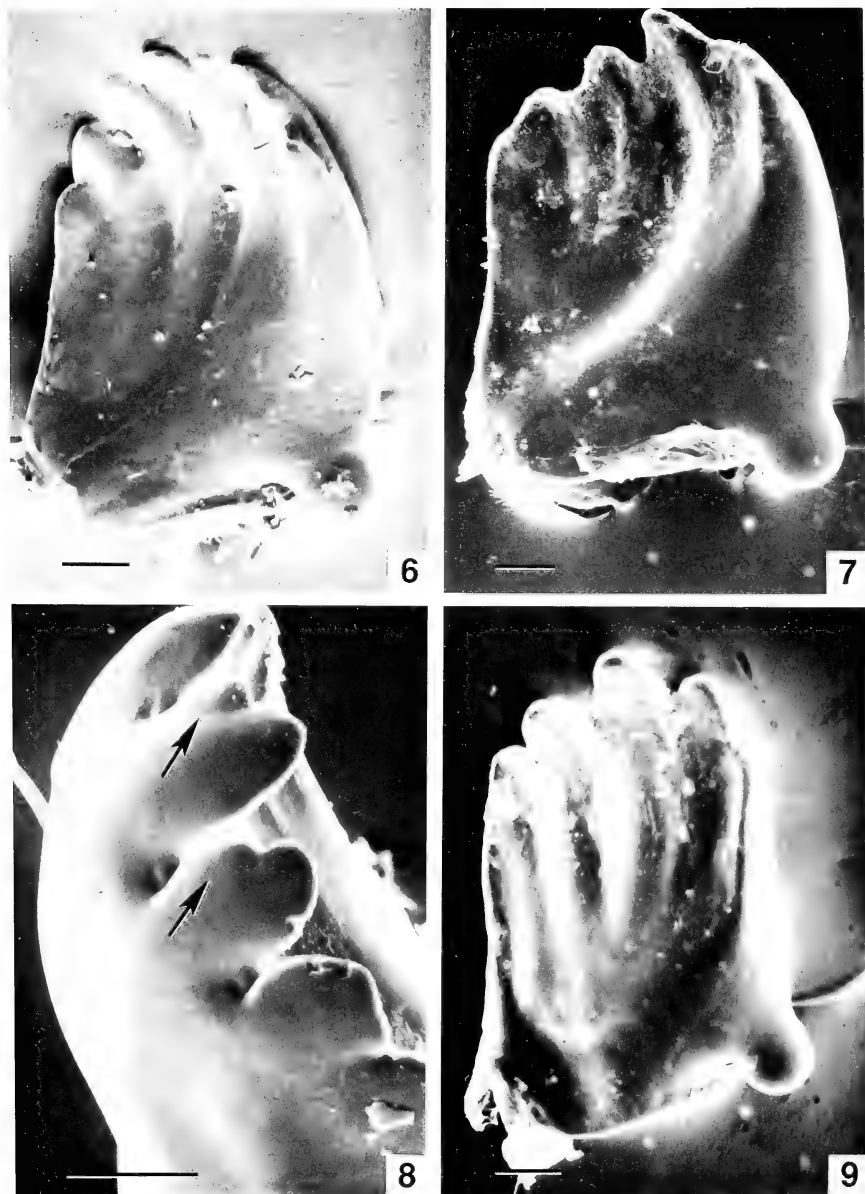
FIGS. 1-2. 1, Worn and 2, Unworn 3rd instar mandibles of *Heterocampa guttivitta*. Dorsal view of left mandible showing how measurements were taken for analysis of wear. Measurement CI was used to indicate absolute size of mandible. Measurement CT was used to measure wear-related changes.

Description of *Heterocampa guttivitta* Mandibles

The unworn first instar mandible is laterally flattened and has five distinct teeth. These teeth, with the exception of the fifth, are usually pointed. The third and fourth teeth have flanges on the bases of their ventrolateral edges (Fig. 8). The first instar mandible lacks a retinaculum (Figs. 6-8). The teeth are greatly shortened in worn first instar



FIGS. 3-5. Unworn 3rd instar mandible of *Heterocampa guttivitta*. Three views of the left mandible. 3, Oral surface; 4, Dorsal surface; and 5, Lateral surface. A = acetabulum (socket), AdAp = adductor apodeme, C = condyle, DP = distal pits, M1 and M2 = setae, R = retinaculum, T1, T2, T3, T4, and T5 = teeth.



FIGS. 6-9. Oral surfaces of 6, unworn and 7, worn left mandibles of 1st instar *Heterocampa guttivitta*. 8, A view of the proximal end of the left 1st instar *Heterocampa guttivitta* mandible shows the flanges (arrows) on ventral-lateral sides of teeth 3 and 4; 9, Oral surfaces of worn left mandibles of 1st instar *Heterocampa subrotata*. Micron bar = 20 microns.

mandibles, however, they are usually still discernable. Usually, the cuticle on much of the oral surface appears rough (Fig. 7). This roughness is probably a result of wear on the cuticle.

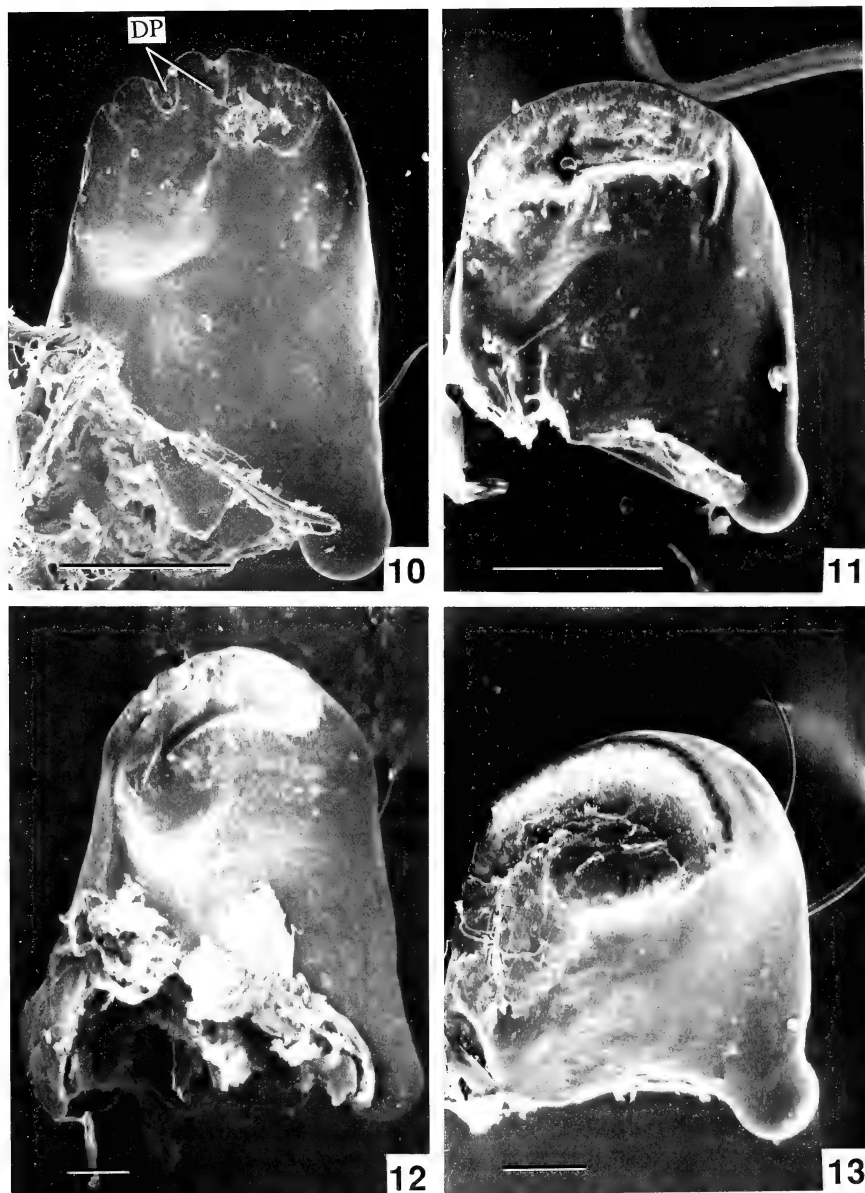
Second instar mandibles have five truncate teeth (Fig. 10). Teeth one and two are not very distinct from one another and often appear fused. The fifth tooth has a series of ridges on its inner surface. There are two distal pits (Fig. 10) on the mandible's oral surface that lie between teeth two and three, and three and four. The second instar mandible is laterally flattened, but the presence of a retinaculum makes it appear more robust than the first instar mandible. The retinaculum is a simple ridge with several dentes at the dorsal end. The retinaculum is worn smooth, often to the point that there is little or no concavity between it and the outer cutting edge (Fig. 11). The cutting edge wears to a smooth, continuous edge. Instars three through five appear to wear in a manner similar to that of the second instar.

The third instar mandible has four truncate teeth (Fig. 12). The first tooth is broad and smooth and may be the result of the fusion of two teeth. The fourth tooth is crenulate. In this instar, there are distal pits between teeth one and two, two and three, and three and four. The distal end of the mandible is curved at approximately a 90 degree angle, causing the cutting edge to be projected mediad. This angle makes the third instar mandible appear more robust than the second instar mandible. The retinaculum is a simple crenulate ridge.

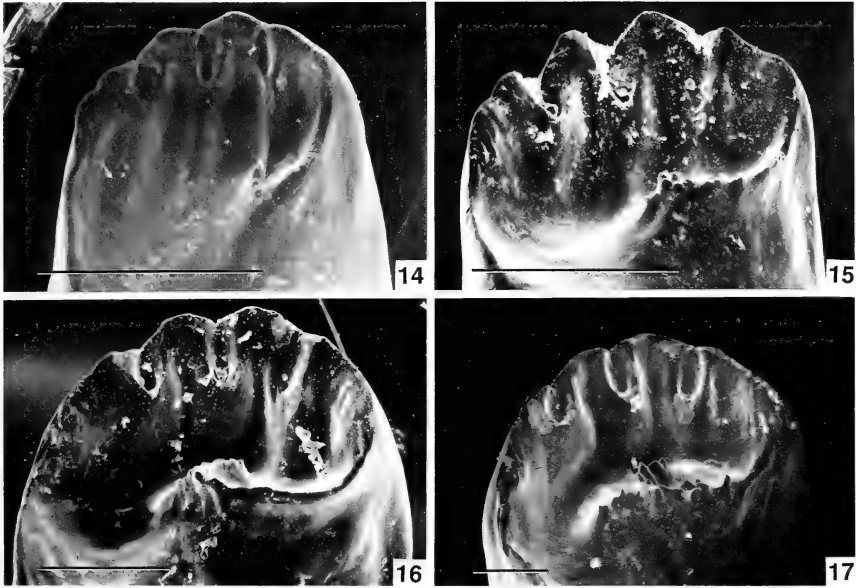
The fourth and fifth instar mandibles are very similar to those of the third instar, except that the distal teeth are not as distinctly separate. The crenae on the retinaculum of the fifth instar mandible are quite small and, in some cases, the retinaculum appears almost smooth.

Description of *Heterocampa subrotata* Mandibles

The unworn and worn mandibles of *H. subrotata* appear very similar to those of *H. guttivitta* with the following exceptions. *H. subrotata* mandibles are smaller than those of *H. guttivitta* (Table 1) and the retinaculum is strikingly different. The retinaculum of the second instar mandible is quite small and has a "hook" at the end. The surface of the retinaculum is irregular. Occasionally, there are cone-shaped projections located on the retinaculum (Fig. 14). There are five, short, rather pointed teeth on the third instar mandible (Fig. 15). The dorsal end of the retinaculum has a series of cone-shaped projections. The arrangement of these projections makes the end of the retinaculum appear bifurcate. The height and number of these projections are variable. However, the location of each projection in relation to the other projections appears to be fixed. The retinaculum of the fourth instar mandible ends in a definite bifurcation (Fig. 16). The branches of the



FIGS. 10-13. Oral surfaces of 10, unworn and 11, worn left mandibles of 2nd instar *Heterocampa guttivitta*. Distal pits (DP) are located between teeth two and three, and three and four of the unworn mandible. The concavity between the distal cutting edge and the retinaculum is greatly reduced in the worn mandible. Oral surface of 4th instar mandibles of 12, *Heterocampa guttivitta* (unworn) and 13, *H. subrotata* (worn). Micron bar = 100 microns.



FIGS. 14–17. Distal end of unworn mandibles of 14, 2nd instar; 15, 3rd instar; 16, 4th instar; and 17, 5th instar *Heterocampa subrotata*. Micron bar = 100 microns.

retinaculum and the retinaculum for a short distance before the bifurcation are crenate. Some of the crenae are fairly sharp. The fifth instar mandible (Fig. 17) differs from the fourth instar mandible in that its retinaculum is dentate its entire length and is more strongly bifurcate.

Right Mandible Versus Left Mandible

The results from the paired *t*-test showed that there was no statistically significant difference ($P > 0.10$) between RCT and LCT or between RCI and LCI for unworn or worn mandibles of *H. guttivitta* at the level of $P = 0.10$, except between the 5th instar RCI and LCI measurements for unworn ($P = 0.0669$) and worn ($P = 0.0422$) mandibles. There was no statistically significant difference ($P > 0.10$) between RCT and LCT or between RCI and LCI for unworn mandibles of *H. subrotata*. No significant difference ($P > 0.10$) for 6 out of 10 measurements was found between RCT and LCT or between RCI and LCI for worn mandibles of *H. subrotata*. The four exceptions were as follows: 1st instar RCT vs. LCT ($P = 0.0137$), 2nd instar RCI vs. LCI ($P = 0.0891$), 4th instar RCT vs. LCT ($P = 0.0380$), 5th instar RCI vs. LCI ($P = 0.0294$). No major morphological differences between the left and right mandibles were found (Dockter 1991). Therefore, only the

TABLE 1. The length of unworn and worn left mandibles of *Heterocampa guttioides* and *H. subrotata*. The measurement (CT), in mm, is from the condyle to the tip of the second tooth (Fig. 1).

Species/instar	Unworn				Worn			
	Range	Mean	SD	n	Range	Mean ^a	SD	n
<i>H. guttioides</i>								
1	0.160-0.171	0.165	0.003	8	0.140-0.165	0.156 ^b	0.008	12
2	0.314-0.342	0.330	0.011	9	0.257-0.296	0.276	0.011	12
3	0.473-0.593	0.546	0.034	11	0.410-0.490	0.447	0.021	12
4	0.792-0.940	0.858	0.037	12	0.618-0.774	0.715	0.040	13
5	1.340-1.541	1.419	0.052	11	1.039-1.206	1.128	0.066	6
<i>H. subrotata</i>								
1	0.143-0.160	0.153	0.007	6	0.134-0.154	0.145 ^c	0.006	12
2	0.239-0.285	0.266	0.012	12	0.217-0.245	0.230	0.010	12
3	0.376-0.439	0.404	0.019	12	0.302-0.371	0.348	0.018	15
4	0.592-0.661	0.631	0.020	12	0.479-0.557	0.526	0.023	15
5	0.938-1.039	0.985	0.039	12	0.748-0.896	0.796	0.051	11

^a All means for worn mandibles were significantly different from means for unworn mandibles at the level of 0.0001 unless otherwise noted.

^b Significantly different at 0.01 ($P = 0.0015$).

^c Significantly different at 0.05 ($P = 0.0284$).

TABLE 2. The width of left mandibles as measured from the condyle to the adductor apodeme (Fig. 1) for *Heterocampa guttivitta* and *H. subrotata*. The measurements (CI), in mm, of unworn and worn mandibles are combined for each instar of each species.

Species/instar	Range	Mean ^a	SD	n
<i>H. guttivitta</i>				
1	0.108–0.120	0.113 ^b	0.003	20
2	0.251–0.279	0.262	0.008	21
3	0.393–0.473	0.436	0.019	23
4	0.626–0.748	0.684	0.028	25
5	1.005–1.139	1.054	0.045	17
<i>H. subrotata</i>				
1	0.097–0.114	0.104	0.005	18
2	0.182–0.222	0.203 ^b	0.010	24
3	0.285–0.348	0.318	0.017	27
4	0.444–0.531	0.493 ^b	0.023	27
5	0.687–0.792	0.730	0.026	23

^a All means for worn mandibles were not significantly different from means for unworn mandibles at the level of 0.05 unless otherwise noted.
^b Significantly different at 0.05 but not at 0.01 (P = 0.0140, P = 0.0413, P = 0.0474, respectively).

left mandible was used for quantitative and qualitative descriptions in this paper (Tables 1–2).

Mandible Wear

First instar mandibles of both *Heterocampa* species were reduced in length by at least 5.2 to 5.5% (Table 3). The amount of wear increased in the second instar to 13.5 to 16.4% (Table 3). Mandible lengths of the final larval instar mandible are reduced by 19.2 to 20.5% (Table 3). The LCT length for larval mandibles from newly molted larvae of *H.*

TABLE 3. The percent of unworn mandible length that is lost during a larval instar for *Heterocampa guttivitta* and *H. subrotata*. Means from Table 1 were used to calculate percent length lost.

Species/instar	% length lost
<i>H. guttivitta</i>	
1	5.5
2	16.4
3	18.1
4	16.7
5	20.5
<i>H. subrotata</i>	
1	5.2
2	13.5
3	13.9
4	16.6
5	19.2

guttivitta was significantly longer ($P < 0.01$) than the LCT length of *H. guttivitta* mandibles taken from the exuviae (Table 1). Unworn LCT length of *H. subrotata* was also significantly longer ($P < 0.01$) than worn LCT length (Table 1). There was no statistically significant difference ($P < 0.01$) between unworn and worn LCI in *H. guttivitta* or in *H. subrotata* (Table 2). A worn mandible surface appears strikingly different from that of an unworn surface. At relatively low magnifications ($\times 300$), an unworn surface appears smooth in contrast to the rough surface of a worn mandible. High magnification of a worn mandible (Figs. 18–19) demonstrates that portions of the cuticle are flaked from the surface.

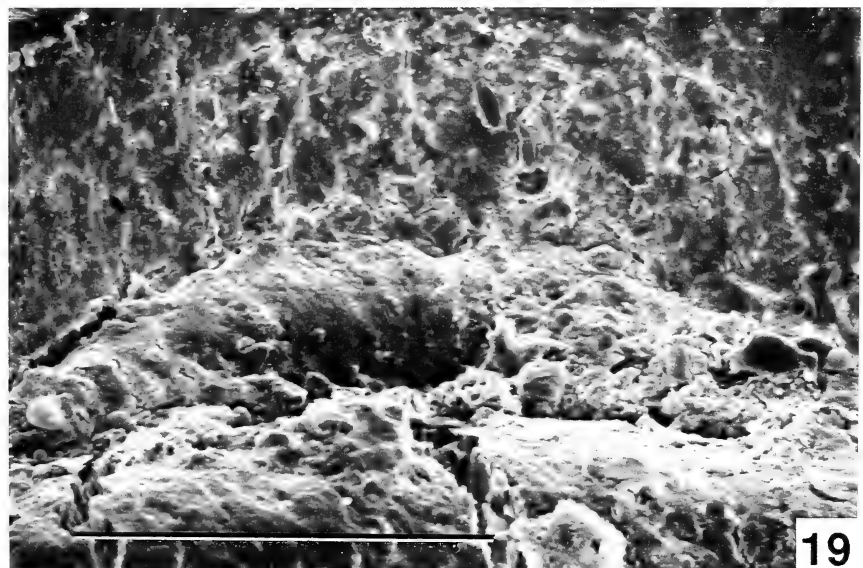
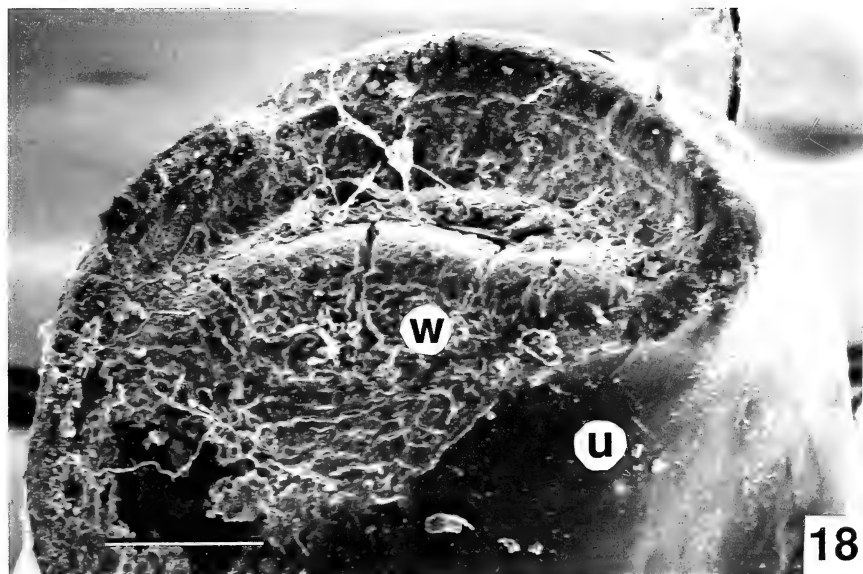
The absolute difference between the length (CT) of unworn and worn mandibles does not represent the actual amount of cuticle loss due to wear. The amounts of wear reported in this study are conservative because there is a bend between the proximal and distal ends of the mandible. It is not possible to compare amounts of wear between species or instars from the data collected in this study because the angle between the proximal and distal areas varies between instars, and especially between species. The difference between unworn LCT and worn LCT becomes more representative of actual cuticle loss as the angle between the proximal and distal areas increases.

DISCUSSION

Developmental and Behavioral Changes Within Species

The change from a shovel-shaped first instar mandible that has a sharply serrate distal margin but lacks a retinaculum, to a second instar mandible that is more robust at the mid- and proximal areas and bears a retinaculum, is associated with a change in feeding habits. This change occurs in both *Heterocampa guttivitta* and *H. subrotata*.

The following description of feeding behavior is based on observations made in the laboratory during the course of the present study. First instar larvae are leaf skeletonizers: they feed on the lower (occasionally upper) epidermis of the leaf while leaving the rest of the leaf tissue intact. The first instar uses the sharp serrations on the mandible to break through the epidermis. The head is quickly and forcefully tilted slightly to one side. This motion is repeated at the same spot on the leaf until the mandible penetrates the epidermis. Once the epidermis is broken a mandible is slid through the leaf tissue and the mandibles are closed to break off a piece of the leaf. Second instar larvae begin feeding on the leaf edge and bite through its entire thickness. During the early part of the second instar, larvae avoid the major veins, but toward the end of this instar, they eat through almost all veins except the midvein.



FIGS. 18-19. **18**, Detail of distal end of worn 4th instar *Heterocampa guttivitta* left mandible. Note the difference between unworn (u) and worn (w) cuticle. **19**, High magnification of worn area of same mandible. Micron bar = 100 microns.

A discussion of the structural changes of the mouthparts (especially mandibles) and the behavioral differences associated with them for two other species of notodontids can be found in Godfrey (1991).

The teeth on the cutting edge become more truncate and less sharply defined with successive instars in both species studied. The amount of pressure needed to break through the leaf tissue is a function of the amount of force exerted per unit area. Pressure can be increased by reducing the area over which the force is exerted or by increasing the force. When the larvae are small, a sharp tooth may be important to increase pressure so that the leaf tissue can be penetrated. As the larvae get larger, the muscles are capable of producing more force, and the extra pressure generated by a sharper more pointed edge may become unnecessary.

Developmental and Behavioral Changes Between Species

The ontogenetic development of the retinaculum in *H. subrotata* is quite different from that in *H. guttivitta*. The retinaculum on the mandibles of *H. subrotata* has a more intricate pattern than the retinaculum of *H. guttivitta*. *H. subrotata* feeds on a more succulent host (northern hackberry) than *H. guttivitta* (white oak). Bernays and Janzen (1988) found a correlation between host texture and mandible morphology. They found that sphingids, which tend to feed on rather succulent leaves, have mandibles that are "long, toothed, and ridged in a variety of complex ways," whereas saturniids have "short and simple" mandibles and feed on "old, tough tannin-rich leaves." The present study tends to support the findings of Bernays and Janzen (1988).

However, more work needs to be done in this area. It would be interesting to determine if the larvae *Nemoria arizonaria* Grote (Geometridae), which exhibit caterpillar morphs that feed on two very different tissues of the same host, also show a change in mandibular structure to best exploit the host tissue. Greene (1989), in his work with *N. arizonaria*, found that the catkin morph, which is a pollen feeder, has a smaller head and jaws (mandibles) than the twig morph, which feeds on "leathery" oak leaves. Bernays (1986) found that head mass and mandible mass were significantly greater in grass-feeding lepidopterous larvae which feed on a tougher diet. One might assume that cuticle production increases when the size of the head and jaw (mandible) increases. It may be that the same factors that control these changes in allometry may also trigger mandibular polymorphisms: if mandibular polymorphisms are in fact shown to exist.

An advantage of an intricate retinaculum is that it may allow the host tissue to be broken into smaller pieces than would be possible with a more simple retinaculum. Bernays and Janzen (1988) indicate that

the smaller the pieces produced by the biting process, the more nutrients that could be extracted from a given amount of tissue, because there is no further mechanical breakdown of food in the gut. However, Bernays (1991) in response to Barbehenn's (1989) study which found that bite size was not correlated with digestibility, concludes that handling time may be more important than bite size. Bernays (1991) states, "Tough leaves are efficiently handled by the snipping, scissor action, whereas the softer more flaccid leaves are more efficiently ingested by the tearing, crushing action".

Mandibular Characters in Systematics

Godfrey et al. (1989) used the presence or absence of teeth on the mandible's distal edge to make hypotheses about phylogenetic relationships among notodontids. However, before systematic (phylogenetic) decisions are made or characters are described with respect to mandibles, one must be certain that unworn mandibles are being examined, especially when a character is easily altered by wear. Nevertheless, for the purpose of identification of caterpillars, it is necessary to describe the most common form of the mandibles, which is often the worn condition in field-collected larvae.

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DESIGNATION OF A LECTOTYPE OF
NISONIADES SOMNUS AND NOTES ON THE
OCCURRENCE OF *ERYNNIS ICELUS* IN
FLORIDA (HESPERIIDAE)

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ABSTRACT. *Nisoniades somnus* Lintner was described in 1881 from one male and one female from "Indian River, Florida." Neither specimen was identified as the holotype, therefore a lectotype and paralectotype are hereby designated. Dubious reports of *Erynnis icelus* from Florida also are examined.

Additional key words: *Erynnis brizo*, type locality, paralectotype.

Over a century ago, J. A. Lintner described a distinctive Floridian skipper as *Nisoniades somnus* (Lintner 1881). This taxon currently is considered a subspecies of *Erynnis brizo* (Boisduval & LeConte) and is restricted to the Florida peninsula (Burns 1964). The description was based on one male and one female from "Indian River, Florida" (given ambiguously as "Florida" by Miller and Brown [1981]) deposited in the collection of W. H. Edwards. The types were undoubtedly collected by Dr. William Wittfeld (1827-1913) and/or his daughter Annie M. Wittfeld (1865-88) of Georgiana, Brevard County, Florida, who were regular correspondents of Edwards and the source of his "Indian River" records. The Wittfelds began collecting Lepidoptera for Edwards in 1880 (dos Passos 1951), thus the specimens probably were captured during the spring of 1880 or 1881.

In his original description, Lintner compared *somnus* almost exclusively to *Erynnis icelus* (Scudder & Burgess), rather than *E. brizo*. As a result, subsequent authors (e.g., Edwards 1884, Skinner 1898, Dyar 1902, Smith 1891, 1903) associated *somnus* more closely with *E. icelus*, alluding to a relationship between the two. This perceived relationship is surprising considering that Lintner (1881) himself revealed in the same paper that males of both *somnus* and *E. brizo* lack hair tufts on the hind tibiae, a structure present in *E. icelus*. Blatchley (1902) summarized the general opinion regarding these taxa when he remarked that *somnus* was "closely allied" to *E. icelus* and "may be only a large southern form."

For many years following its original description, *somnus* was known from very few localities and most authors (e.g., French 1885, Maynard 1891, Skinner 1898) continued to list this taxon only from the type locality. An exception was Scudder (1889) who listed "*Thanaos brizo*"

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from Florida and included the additional locality of "Haulover." This record was provided by E. A. Schwarz, probably as a result of his visits to Florida in 1875 and 1876 (Schwarz 1888). This reference is especially interesting because Haulover formerly existed in northern Brevard County, approximately 22 km north of Georgiana, where the type specimens of *N. somnus* probably originated. Schwarz obviously recognized the similarity of his specimens to *E. brizo* and identified them as such. This was the first glimpse into the true relationship between these taxa.

Dyar (1905) was the first to openly suggest that *somnus* was "perhaps but a dark form of *brizo*" and noted the resemblance of their genitalia. This notion was supported by Skinner (1914) who also commented on the similarity of their genitalia. F. E. Watson (in Grossbeck 1917) more confidently submitted that *somnus* is "probably a subspecies of *brizo*." Following the acceptance of *somnus* as a subspecies of *E. brizo* by Barnes and McDunnough (1917), this taxonomic status was generally adopted. However, Holland (1931) stated that he was "unable to agree with this opinion" and retained the mistaken belief that *somnus* was "much nearer to *T. icelus*."

Lintner (1881) did not designate either of his specimens of *Nisoniades somnus* as the holotype. Miller and Brown (1981) were unaware of the location of Lintner's syntypes although Skinner (1914) stated that they were deposited in the Carnegie Museum of Natural History, where they remain today. These specimens were figured by Holland (1931: plate 51, figs. 3–4) who identified each as "type." Both specimens lack antennae (the male retains a portion of the left antenna) which were noticeably drawn onto the Holland figures. The specimens are in good condition, except the abdomen of the female is now detached and pinned with the specimen in a dry vial. The male specimen (Fig. 1) (left forewing length, base to apex = 15 mm) is hereby designated as the lectotype. It bears three labels: "Nisoniades/Somnus, ♂/Lintn./TYPE." in Lintner's hand; "Collection/W. H. Edwards" printed; and "Butterfly Book/Pl. 51 Fig. 3," printed and handwritten. I have affixed a red label declaring the specimen as the lectotype. The female specimen (Fig. 2) (left forewing length, base to apex = 16 mm) is designated as a paralectotype. It also bears three labels: "Nisoniades/ Somnus, ♀/Lintn./ TYPE." in Lintner's hand; "Collection/W. H. Edwards" printed; and "Butterfly Book/Pl. 51 Fig. 4," printed and handwritten. A red label has been affixed to indicate its status as paralectotype. The type locality is restricted to Georgiana, approximately 5 km south of the city of Merritt Island, Brevard County, Florida. An additional male specimen of *E. b. somnus* was figured by Holland (1898, 1931: plate 48, fig. 2). This specimen, from the W. H. Edwards collection, is labelled



Nisoniades
Somnus ♂
Lintn.
TYPE.

Collection
W. H. Edwards

Butterfly Book
Pl. 57 Fig. 3

1



Nisoniades
Somnus ♀
Lintn.
TYPE.

Collection
W. H. Edwards

Butterfly Book
Pl. 57 Fig. 4

2

FIGS. 1-2. *Nisoniades somnus* Lintner. 1, Lectotype male; 2, Paralectotype female.

in Edwards' hand as "*somnus*/♂/Ind. Riv." and is considered a topotype.

Unlike most of Edwards' specimens, the types of *N. somnus* do not possess locality data. Edwards did not place labels on his individual specimens until he sold his collection to W. J. Holland in the late 1880's (Brown 1964). At that time, he prepared labels that typically included the name of the species, sex of the specimen and a brief (sometimes cryptic) mention of the location of capture. Edwards probably did not affix such labels to the *N. somnus* types because Lintner's labels already were present.

The difficulty experienced by most nineteenth century lepidopterists in recognizing distinct differences between *E. b. somnus* and *E. icelus* contributed to confusion over the distribution of *E. icelus* that haunted the literature for 80 years. Edwards (1884) casually listed *E. icelus* from "Fla," regardless of the fact that his closest record was from Illinois. Subsequent authors, including French (1885), Maynard (1891), Skinner (1898) and Holland (1898) followed Edwards and continued to include Florida within the range of *E. icelus*. Scudder (1889) implied a reluctance to accept Florida reports when he remarked that "Edwards also gives it from Florida." Apparently, Scudder had not seen any specimens of *E. icelus* from Florida, nor had he received any such reports from his many correspondents. Blatchley (1902) reported that he collected "several" *E. icelus* (supposedly determined by H. Skinner) in the spring of 1889 at Ormond, Volusia County, Florida (he listed *E. b. somnus*

separately). Not until the treatises on the Hesperioidea by Lindsey (1921) and Lindsey et al. (1931) did the Floridian reports finally become unacceptable. The furthest south from which these authors reported *E. icelus* was North Carolina. However, the saga continued when Macy and Shepard (1941) resurrected the Floridian reports and Evans (1953) indicated that the British Museum (Natural History) contained *E. icelus* from Florida. Forbes (1960) also listed *E. icelus* from Florida, possibly on the authority of Evans. Burns (1964) examined the purported Floridian specimen of *E. icelus* in the British Museum, a dateless male from the R. Oberthür collection marked only as "Floride," and considered it mislabelled. Burns added that "*E. icelus* has often been attributed to Florida, chiefly in older literature; the error seems to stem from Edwards. Many highly questionable locality records (and food-plant records as well) have been uncritically repeated, in literature bearing on the *Erynnis*, to the extent that nowadays they may appear to be reliable, when actually they are not." Although Kimball (1965) included a contemporary record (1961) of *E. icelus* from the Florida panhandle (determined by W. T. M. Forbes as "apparently this") he retorted "I am much in doubt as to whether this species is really native to Florida."

The basis of the early reports of *E. icelus* in Florida probably can be traced to a small female specimen of *E. b. somnus* from the W. H. Edwards collection labelled "Nisoniades/icelus(?)/Lintn./♀/Ind. Riv." in Edwards' hand. The specimen was undoubtedly collected by the Wittfelds at Georgiana, Brevard County, Florida at about the same time the types of *Nisoniades somnus* were collected (ca. 1880). This supports Skinner (1914) who suggested that Floridian records of *E. icelus* may actually be *E. b. somnus*. Improperly identified skippers are epidemic within early collections and even remotely similar species were confused. This problem is exemplified by H. G. Dyar who determined as *E. b. somnus* a Mississippi specimen of *Erynnis zarucco* (Lucas) (Burns 1964). However, this inherent identification problem does not entirely solve the Floridian *E. icelus* dilemma.

Six male specimens of *E. icelus*, bearing handwritten and printed labels reading "Fla" from the W. J. Holland collection, are deposited in the Carnegie Museum of Natural History (identifications verified by genitalic examination). Three of these specimens also possess handwritten labels reading "Morrison," apparently in reference to the nineteenth century collector Herbert K. Morrison. Morrison collected in Florida in 1883, 1884 and 1885 (Essig 1931). Morrison also visited at least ten other states between 1874 and 1883 (Essig 1931), all of which possess valid records of *E. icelus* (Burns 1964). Morrison was a prolific collector and such zeal increases the potential for accidental mislabel-

ling. Nonetheless, the validity of these specimens is difficult to ascertain, especially since no similarly labelled specimens in the Carnegie Museum are thought to be mislabelled (J. E. Rawlins pers. comm.). These six specimens are probably the basis for Holland's (1898, 1931) inclusion of Florida within the range of *E. icelus*.

There is a very remote possibility that *E. icelus* occurred (or occurs) in northern Florida, especially the panhandle where habitats of more northern affinities occur. However, valid specimens of this species are not known from south of northern Georgia (Burns 1964, Opler & Krizek 1984). Unless additional evidence is revealed, the six Floridian specimens of *E. icelus* will remain an enigma.

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I am grateful to John E. Rawlins of the Carnegie Museum of Natural History for helpful information and the loan of specimens. Thanks are also extended to Timothy L. McCabe of the New York State Museum for his verification of J. A. Lintner's handwriting. John M. Burns and an anonymous reviewer critically reviewed the manuscript and provided many helpful suggestions.

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FIRST NORTH AMERICAN RECORDS OF
EPINOTIA ABBREVIANA (TORTRICIDAE),
A EUROPEAN PEST OF *ULMUS* SPECIES

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ABSTRACT. *Epinotia abbreviana* (Fabricius), recently found established in Newfoundland, Canada, is described and diagnosed, with illustrations of genitalia and wings.

Additional key words: diagnosis, distribution, host plant, genital structure, Newfoundland.

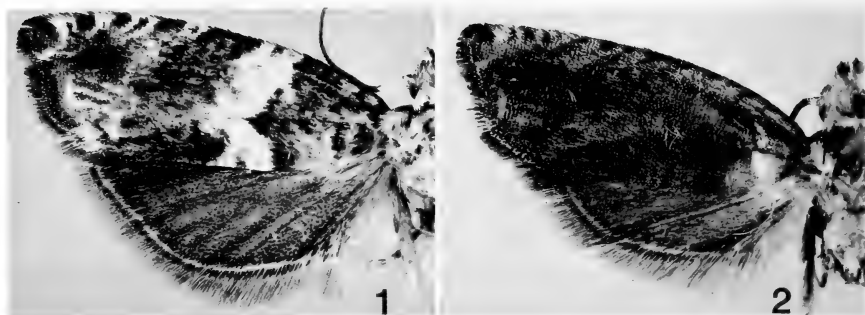
Epinotia abbreviana (Fabricius) is native to Europe. The larval stages of this species feed on various species of *Ulmus* (Ulmaceae). Two male specimens were reared from larvae collected in 1981 on elm in St. John's, Newfoundland, Canada; in 1988 two females were reared from larvae collected on *Ulmus rubra* Muhl. in Bowring Park, St. John's. The second collection indicates that this species has become established in the area.

Both series of specimens were collected by personnel of the Forest Insect and Disease Survey (FIDS) from Forestry Canada's Newfoundland and Labrador Region. The species was identified by the author based on detailed examinations of all four specimens. Specimens collected from England (1 ♂) and Germany (1 ♀) also were examined to lend further support to the identification.

The description, illustrations, photographs, and review of biological aspects of this species provided in this article will help researchers to recognize and identify the pest. This information will be particularly useful for surveying and monitoring the species in St. John's and neighboring areas. Descriptions and illustrations of various morphological aspects of the species also can be found in Bradley et al. (1979), Kuznetsov (1978), Graaf Bentinck and Diakonoff (1968), Hannemann (1961), Benander (1950), Pierce and Metcalfe (1922), and Kennel (1921).

DIAGNOSTIC FEATURES

Description. *Epinotia abbreviana* is a variable species. The forewing of specimens collected in Newfoundland exhibits the two extremes of variation, which ranges from a pale form with distinct and contrasting markings to a dark form with an almost uniform dark gray-brown forewing and faint markings. Bradley et al. (1979) provided a series of wing illustrations showing the variability of this species in England. The ISCC-NBS (Inter-Society Color Council-National Bureau of Stan-



FIGS. 1-2. Dorsal aspect of *E. abbreviana* adults; 1, form 1; 2, form 2.

dards) Color-Name Charts (Kelly & Judd 1955) are used in the following descriptions.

Head. Vertex, antenna medium brown to dark gray-brown. Frons white. Labial palpus medium brown on apical third, other areas yellow-white to white.

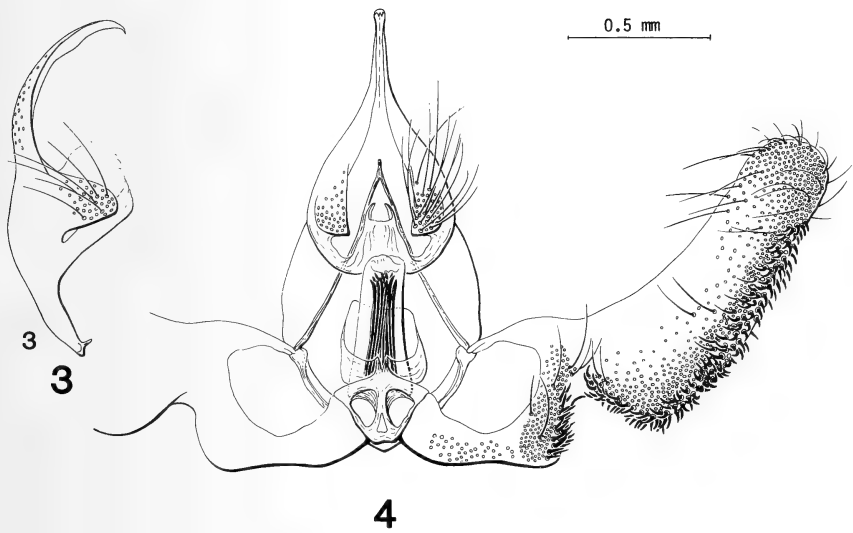
Thorax. Notum yellow-brown to dark gray-brown. Pleural area yellow-white. Forewing 7.0-7.5 mm long, without costal fold. *Form 1* (Fig. 1): Forewing mostly medium brown; area between medial fascia and basal patch yellow-white, extended across wing, shaped like "greater-than" or "less-than" sign; costal strigulae well defined, with alternating yellow-white and medium brown comma-shaped spots; area between postmedial and subterminal fasciae, and that between subterminal and terminal fasciae, narrow, silver-gray, extending from dorsal end of terminal margin to costal margin at two-thirds length from wing base, and from terminal margin at one-fourth length from wing apex to costal margin at three-fourths length from wing base, respectively; tornal area with silver-gray ocellus. *Form 2* (Fig. 2): Forewing medium brown in most areas, fasciae obsolete; as with form 1, tornal ocellus and two oblique lines in areas between postmedial and terminal fasciae silver-gray, but faintly visible; costal strigulae dull, consisting of alternating yellow-brown and medium brown spots. Hindwing uniform gray-brown; fringe paler. *Form 3*: Similar to form 2, except much darker, dark gray-brown. Legs in all forms with fore- and midlegs medium brown, except basal and apical margins of femur, tibia, tarsomeres, and mid area of tibia white; hindleg yellow-white, except tarsomeres medium brown basally.

Abdomen. Medium brown to dark gray-brown dorsally.

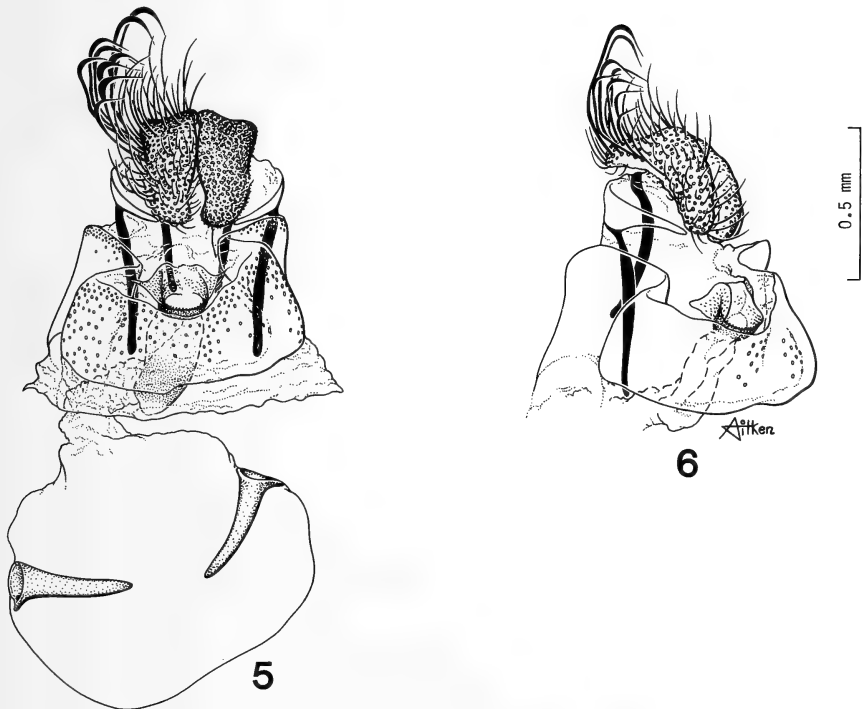
Male genitalia (Figs. 3-4): Mesal surface of valva with numerous, short, stout setae along ventral margin of sacculus, and with slender, dorsally directed setae on remaining areas. Tegumen well developed, triangular. Uncus long and slender, gradually tapered apically, gently curved ventrally, with small, inconspicuous bifid apex. Socius well developed, with dense, posterodorsally directed, long setae; apex, as seen laterally, bluntly convex. Aedeagus cylindrical; cornuti long, well sclerotized, distinctly curved apically, 10-11 in number.

Female genitalia (Figs. 5-6): Papillae anales foot-shaped, distinctly arched anterodorsally, fringed laterally with long, hooked setae. Lamella postvaginalis small, densely spiculate. Colliculum long, cylindrical, slightly sclerotized, smooth, as long as non-sclerotized part of ductus bursae. Corpus bursae voluminous, potato-shaped, slightly wider than long, with 2 well-sclerotized, horn-shaped, anteromedially directed signa, one on each side; surface of corpus bursae finely reticulate.

Remarks. The male genitalia of *Epinotia abbreviana* are similar to those of *E. sperana* McDunnough, *E. myricana* McDunnough, *E. ethnica* Heinrich, *E. ulmicola* Kuznetsov, *E. solandriana* (Linnaeus), and



FIGS. 3-4. Male genitalia of *E. abbreviana*; 3, lateral aspect of tegumen, uncus and socius; 4, posteroventral aspect with both valvae spread.



FIGS. 5-6. Female genitalia of *E. abbreviana*; 5, ventral aspect; 6, lateral aspect.

E. trigonella (Linnaeus); the first three species are native to North America, the third is found in south of the Primorye Territory of Russia, and the last two are widespread in the Holarctic region. Specimens of *E. ulmicola* were not available for study. However, according to Kuznetsov (1966), *E. ulmicola* is distinguished from *E. abbreviana* (sensu *E. trimaculana* Donovan) by the following characters: apex of uncus simple, bifid in *E. abbreviana*; distoventral angle of sacculus obtuse in mesal view, approximately 90° in *E. abbreviana*; and apex of socius pointed in lateral view, bluntly convex in *E. abbreviana*. The females of these two species are indistinguishable. All other species mentioned above have a long, fingerlike uncus with a distinctly bifid apex, and valvae with the ventral margin deeply and broadly emarginate at one-third the length from base (Fig. 4). *Epinotia abbreviana* is distinguished by the following characters: 1) costal fold of forewing absent, present in others; 2) uncus at least as long as aedeagus, shorter in others; and 3) apex of socius bluntly convex in lateral view, pointed in others. The female is characterized by the distinct, dorsoanteriorly arched papillae anales, which are fringed laterally with large, slender, hooked setae; by the lamella postvaginalis with an acute dorsolateral angle on each side; and by a pair of large, horn-shaped signa.

Material studied. CANADA: Newfoundland: St. John's, em. 18, 21.VI.1981, elm, (FIDS), 2 ♂; Bowring Park, St. John's, em. 6-7.VII.1988, *Ulmus rubra*, (FIDS), 2 ♀, all in CNC. ENGLAND: Abingdon, 30.VI.1924, (H. C. Hayward), 1 ♂, in USNM. GERMANY: Nieder-Weser, Bremen-Stadtwald, 5.VII.1941, *Ulmus*, (E. Jackh), 1 ♀, in USNM.

Distribution and biology. *Epinotia abbreviana* is widespread and distributed throughout Europe and Asia Minor. Early larval instars of this species feed inside the developing bud of species of *Ulmus*. A characteristic ring of small perforations appears on the leaf surface when the leaf becomes fully expanded in the spring; Bradley et al. (1979) provided excellent illustrations of leaves of *Ulmus* damaged by the larvae. Later larval instars become leaf tiers. *Epinotia abbreviana* is a potential pest of *Ulmus* species in Canada and the United States.

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I thank Kevin Pardy of the Newfoundland and Labrador Region, Forestry Canada for providing collection information and specimens of *E. abbreviana* collected in St. John's, and R. W. Hodges of the United States National Museum of Natural History, Washington, D.C., for the loan of specimens of *E. abbreviana* from Europe.

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A REVISION OF THE SPECIES OF *NEMATOCAMPA*
(GEOMETRIDAE: ENNOMINAE) OCCURRING
IN THE UNITED STATES AND CANADA

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ABSTRACT. The three nearctic species of *Nematocampa* are revised, with special emphasis on the biology and complex nomenclatural history of the type species, *N. resistaria* (Herrich-Schäffer, 1855). Of the two names most commonly applied to this species, *limbata* Haworth, 1809, is a primary homonym, and *filamentaria* Guenée, 1857, is a junior synonym of *resistaria*. *Nematocampa resistaria* is transcontinental; *N. brehmeata* (Grossbeck, 1907) is limited to California; *N. baggettaria*, new species, is south-eastern; and *N. expunctaria* Grote, 1872, is synonymized under *N. resistaria*. The well-known larva of *N. resistaria* feeds on plants of at least 20 families, but the larvae of the others are unknown. About 20 additional species occur in the neotropics.

Additional key words: taxonomy, nomenclature, host plants.

Nematocampa Guenée is a New World genus of at least 23 species, a few of which apparently are undescribed. Although concentrated in the tropics and occurring southward to Argentina, three species are present in the temperate zone of the United States, and one reaches Canada. The neotropical species are diverse and may not all be congeneric. A few other neotropical Ennominae, perhaps most notably *Melinodes conspicua* Schaus from Brasil, have a reticulate wing pattern suggestive of that of *Nematocampa* but are not closely related.

Although the type species, *N. resistaria* (Herrich-Schäffer), has a large literature that goes back to 1809, was found and drawn by John Abbot perhaps even earlier (Abbot drawing copied by Guenée 1857:9, p. xlvi; 1858:pl. 2, fig. 3), and is widely known because of its distinctive appearance and unusual, filament-bearing larva, its nomenclature and taxonomy have not been interpreted correctly. It was described under eight names, two of which, *N. limbata* (Haworth) and *N. filamentaria* Guenée, have competed incorrectly for priority in all of the more recent literature. Despite that long history, another very distinct species of the southeastern U.S. remained undiscovered until the 1980's and is described in this paper.

Originally I intended only to describe this new species, *Nematocampa baggettaria*, and perhaps verify the correct name for the type species. However, the paper assumed the proportions of a revision as more material and more literature were examined, and the full complexity of the problem unfolded. Every name referring to *Nematocampa* species in the fauna of America north of Mexico is here applied differently except that of *N. brehmeata*.

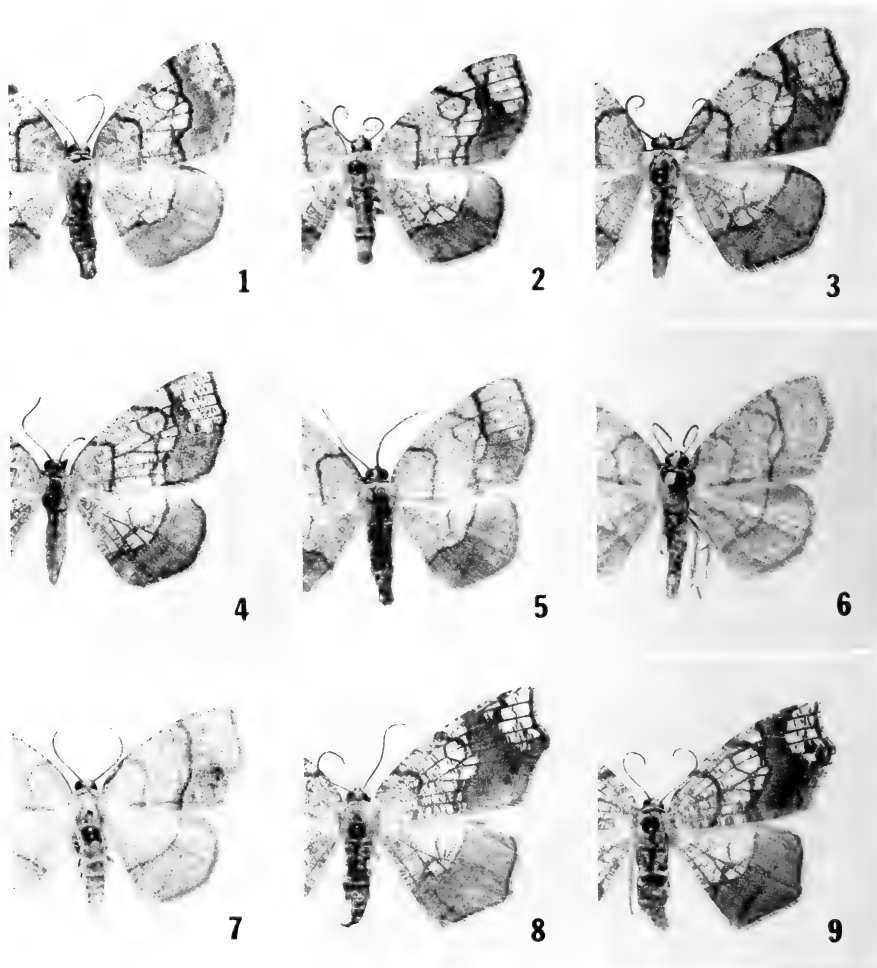
Nematocampa Guenée

Nematocampa Guenée, 1857, in Boisduval and Guenée, Hist. Nat. des Insectes, Species général des Lépidoptères 9:120. Type species: *Nematocampa filamentaria* Guenée, 1857, *ibidem* 9:121; 1858, *ibidem* Atlas:pl. 2, fig. 3; pl. 5, fig. 1, by monotypy. *Nematocampa filamentaria* Guenée is herein regarded as a junior subjective synonym of *Microgonia resistaria* Herrich-Schäffer, 1855, Sammlung Aussereuropäischer Schmetterlinge, p. 41, pl. [65], fig. 368.

Species of this genus may nearly always be recognized by the characteristic wing pattern. The dark medial line of the forewing is unusually far out, partly touching or confluent with the postmedial line (Figs. 1–18), or missing (Figs. 19–23); in *N. resistaria* and *brehmeata* these lines touch near the inner margin and at vein M_2 , thereby making a closed cell between them near the middle of the wing. Neotropical species, however, do not have a well-developed closed cell, or it may not show in poorly marked specimens. The outer third of both wings has conspicuous areas of brown or purplish-brown shading in most species. The pale ground color, varying from whitish to deep orange yellow, is often striated transversely with multiple, fine, short streaks, and marked longitudinally with fine dark lines on the veins, giving a reticulated effect. Length of forewing: ♂♂, 7–14 mm; ♀♀, 7–16 mm.

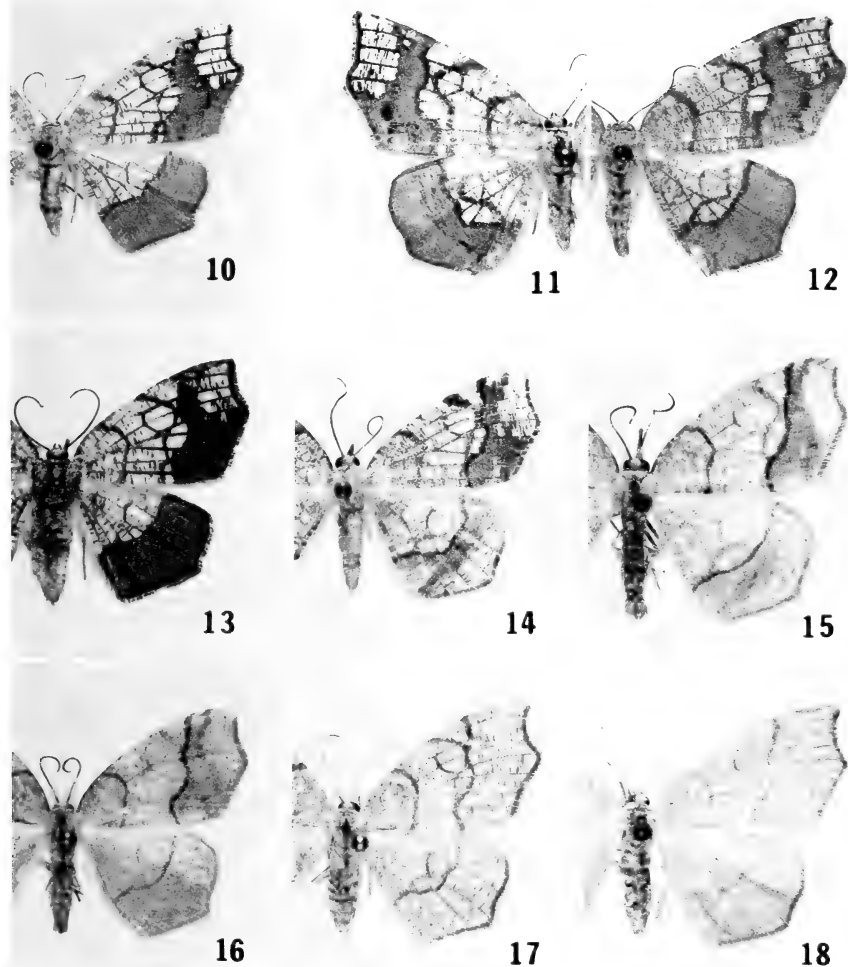
Other features of *Nematocampa* are as follows: male antenna prismatic, compressed, finely setose; female antenna filiform, finely setose; chaetosema small, with 5–6 bristles; front smooth; palpus short, only slightly surpassing front; male hindtibia with inner preapical spur curiously modified in most species (Figs. 24–26), elongated almost to end of tibia and claviform, enlarged distally to 2–4 times thickness of normal, linear spurs.

Male genitalia (Figs. 28–33) with end of gnathos laterally compressed in typical group, dorsoventrally compressed in some neotropical species; juxta large and elongated dorsally (toward uncus), where it becomes notched or bifurcated in all North American species and some neotropical ones; valve in all North American and some neotropical species divided into a long costal lobe and shorter, rounded, saccular lobe, as in Ennominae of the tribe Semiothisini; other neotropical species, presumed to be more primitive ones in this respect, have valve undivided; most neotropical species, those with undivided valve, have a pair of short spinose processes (resembling a furca) arising from juxta, one on each side; in those with a bilobed valve, the spinose processes have degenerated to a pair of simple sclerites flanking juxta and apparently forming narrow bridges between juxta and transtilla. A long, hairy corema (Fig. 28) arises laterally from near the base of each valve in most species, but may be reduced or vestigial (Fig. 30). Female genitalia typically with a longitudinally ovate signum, with an indeterminate number of dentate processes radiating from its margin.

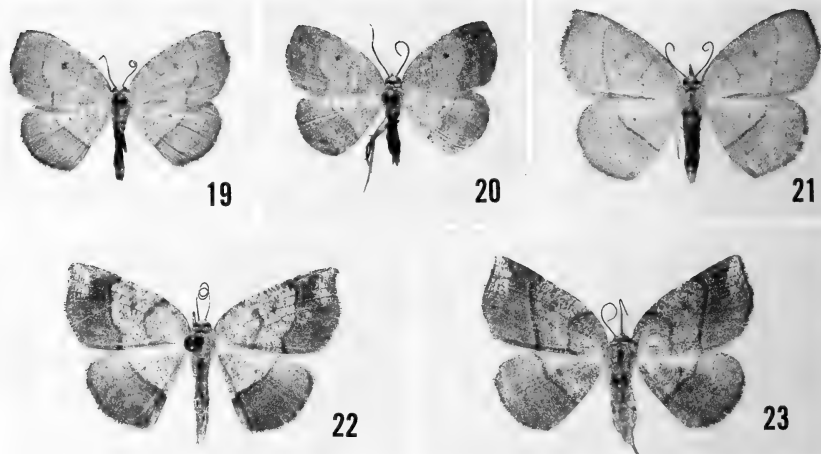


FIGS. 1-9. *Nematocampa resistaria*. 1, ♂, Armdale, Halifax Co., Nova Scotia, 12 Aug. 1948. 2, ♂, Seton Cr., Lillooet, British Columbia, 4 July 1991. 3, ♂, Beaverton, 9 mi W of Portland, Oregon, 14 June 1963, C.W. Nelson. 4, ♂, Oak Zone, 5 mi SW of Midway, Wasatch Co., Utah, 29 July 1971. 5, ♂, Sycamore Landing, nr. Seneca, Montgomery Co., Maryland, 28 May 1977. 6, ♂, McClellanville, Charleston Co., South Carolina, 20 May 1974, R. B. Dominick. 7, ♂, Eagle L., Colorado Co., Texas, 27 April 1978, A. & M. E. Blanchard. 8, ♀, Baddeck Bridge, Victoria Co., Nova Scotia, 29 July 1970. 9, ♀, Sycamore Landing, Seneca, Montgomery Co., Maryland, 24 July 1976. Magnification: 2×.

Remarks. *Nematocampa* in the broad sense has three main species groups. **Group 1**—those with or without a modified hindtibial spur, but always with a bilobed valve, degenerate furca, strongly bifurcate juxta, and one cornutus; group 1 includes the three North American species treated in this revision and two closely related neotropical species



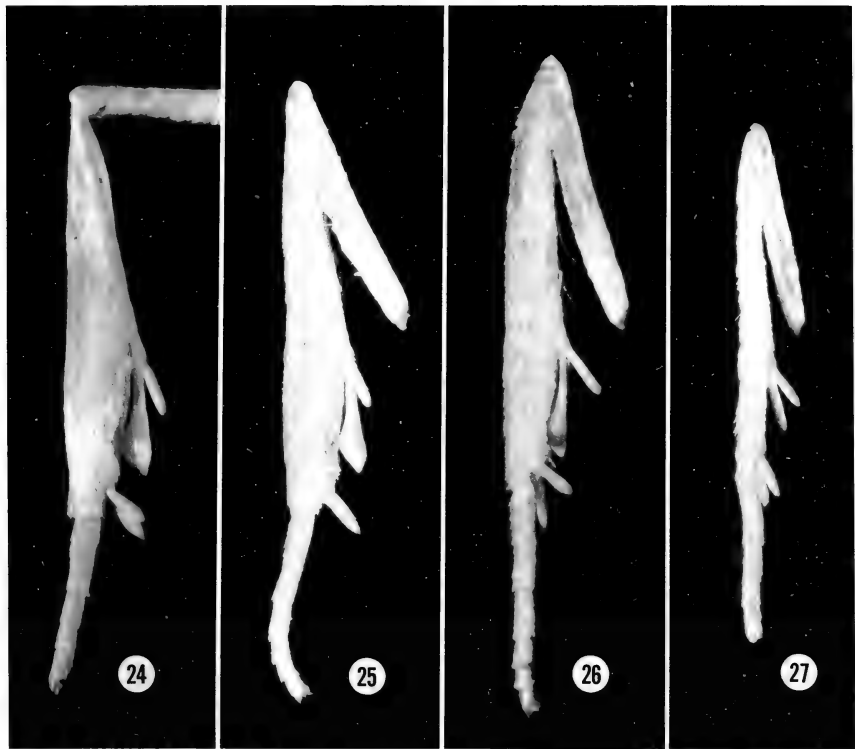
FIGS. 10-18. *Nematocampa* species. **10**, *N. resistaria* ♀, Oak Zone, 5 mi SW of Midway, Wasatch Co., Utah, 29 July 1971. **11**, *N. resistaria* ♀ (white ground color), nr. Elsie, Clatsop Co., Oregon, 2 Sept. 1968, S. G. Jewett. **12**, *N. resistaria* ♀ (yellow ground color), same locality, 6 Sept. 1968, E. L. Griepentrog. **13**, *N. resistaria* ♀, Withlacoochee State Forest, Hernando Co., Florida, reared from larva on *Myrica* 7 May 1983, H. D. Baggett. **14**, *N. brehmeata* ♂, Mt. Shasta (city), Siskiyou Co., California, 1 Aug. 1990. **15**, *N. brehmeata* ♂, Anderson Springs, Lake Co., California, 3 July 1949, W. R. Bauer. **16**, *N. brehmeata* ♂, same data as for Fig. 15. **17**, *N. brehmeata* ♀, same data as for Fig. 15 but collected 26 July 1952. **18**, *N. brehmeata* ♀, San Antonio Cr., Sonoma Co., California, 21 July 1939, W. R. Bauer. Magnification: 2×.



FIGS. 19–23. *N. baggettaria*. 19, Holotype ♂. 20, ♂, 8 mi N of Sumatra, Apalachicola Natl. Forest, Liberty Co., Florida, 2 June 1990, H. D. Baggett. 21, ♂, 4.2 mi NE of Abita Springs, St. Tammany Parish, Louisiana, 25 April 1984 (spring brood), V. A. Brou. 22, ♀, Torreya State Park, Liberty Co., Florida, 19 August 1982, H. D. Baggett. 23, ♀, Same data as for Fig. 21 but collected 14 April 1984 (spring brood). All illustrated specimens are in the collection of the USNM, and all were collected by the author unless otherwise indicated. Magnification: 2×.

that I could identify, namely *N. evanidaria* Schaus and *N. arenosa* Butler (plus other neotropical species apparently undescribed). **Group 2**—the remaining species of similar appearance and with similarly modified hindtibial spur, but with different male genitalia, as follows: valve entire, not two-lobed; juxta not or hardly bifurcate; furca fully developed; and aedeagus with one or two cornuti (*N. completa* Warren, *N. angulifera* Oberthür, *N. reticulata* Butler, *N. decolorata* Warren, and probably others). **Group 3**—a group of three or four species of different appearance, in part with a narrow, dark, outer marginal border only, without a modified hindtibial spur, with simpler male genitalia and reduced juxta, no remnants of a furca, numerous cornuti in the vesica, and many other differences (e.g., some with bipectinate male antennae). This group includes *N. falsa* Warren, *N. confusa* Warren, and possibly *N. benescripta* Warren and *N. interrupta* Warren, although the last two seem different again. There is little to tie group 3 to *Nematocampa*, and these species will almost certainly be removed to other genera after further study. Certain species of other ennomine groups, most notably *Melinodes conspicua* Schaus from Brasil, may have a pattern suggestive of *Nematocampa* but are probably unrelated.

When I prepared the Check List of North American Geometridae (Ferguson 1983), I left *Nematocampa* at the end of the Ennominae

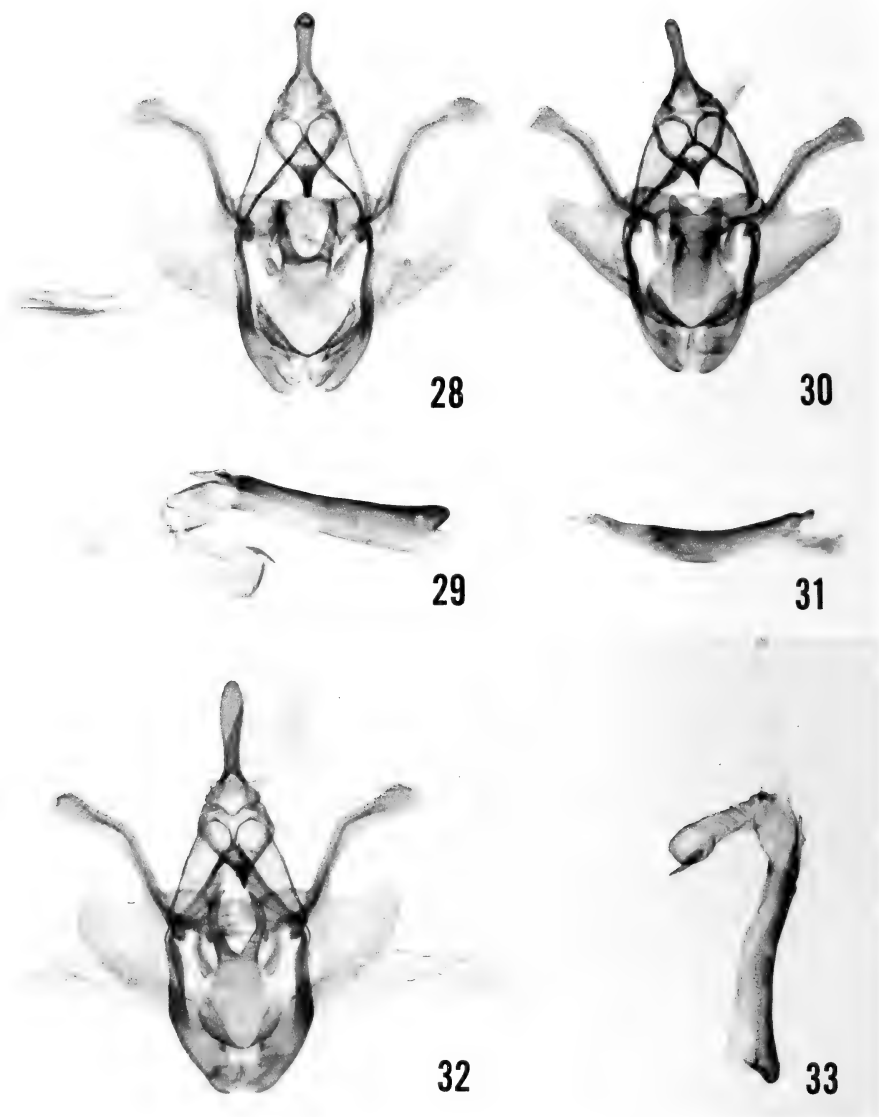


FIGS. 24-27. Male right hindtibiae of *Nematocampa* species. **24**, *N. resistaria*, Okefenokee Swamp, Georgia. **25**, *N. resistaria*, near Elsie, Clatsop Co., Oregon. **26**, *N. brehmeata*, Anderson Springs, Lake Co., California. **27**, *N. baggettaria*. 4.2 mi NE of Abita Springs, St. Tammany Parish, Louisiana.

because, like other authors, I had not determined where it belongs. This has not changed because it would require comprehensive revisionary study of the neotropical Ennominae to determine the phylogenetic relationships of *Nematocampa*.

Key to Species of *Nematocampa* of the United States and Canada

- 1. Male with hindtibia enlarged and inner preapical spur curiously modified, long, clavate (Figs. 24-26); ground color of wings whitish or yellow; wing length generally more than 10 mm; widely distributed 2
- Male with hindtibia not enlarged and preapical spurs unmodified (Fig. 27); ground color of wings orange brown to yellowish; moths small, wing length less than 10 mm; southeastern United States *baggettaria*
- 2. Females with ground color white or nearly so; males with clavate hindtibial spur (Figs. 24, 25) longer than first tarsal segment, conspicuously swollen to 3-4 times thickness of other preapical spur; transcontinental, widespread *resistaria*
- Females with ground color yellow (a few Oregon females of *resistaria* with yellow



FIGS. 28-33. Male genitalia. 28, *N. resistaria*, McMinnville, Oregon. 29, Aedeagus of same specimen. 30, *N. baggettaria*, Jefferson Co., Florida. 31, Aedeagus of same specimen. 32, *N. brehmeata*, Anderson Springs, Lake Co., California. 33, Aedeagus of same specimen.

ground color will key here); males with clavate hindtibial spur (Fig. 26) swollen only to twice thickness of other preapical spur; California *brehmeata*

***Nematocampa resistaria* (Herrich-Schäffer), revised status**

(Figs. 1–13, 24, 25, 28, 29, 34)

Phalaena limbata Haworth, 1809, *Lepidoptera Britannica*, Pt. 2:346. (Publication dates for the four parts of the *Lepidoptera Britannica* were established by Griffin, 1932).

HOMONYM

NOTE: *Phalaena limbata* Haworth is a junior primary homonym of *Phalaena limbata* Linnaeus, 1767, *Systema Naturae*, ed. 12, p. 873, which is the European species now known as *Evergestis limbata* (L.) (Crambidae). According to the International Code of Zoological Nomenclature (1985, Art. 59a), "a species-group name that is a junior primary homonym must be permanently rejected." It is unlikely that the name *limbata* could be conserved because it has not been in continuous use for the past 50 years. Some authors have used the name *filamentaria* Guenée for this species.

Macaria limbata, Stephens 1829(2):155. Wood 1839, 1854:116, pl. 26, fig. 748n.

Ania limbata, Stephens [1831]:322. Hulst 1896:373. Dyar 1902 [1903]:338.

Nematocampa limbata, Barnes and McDunnough 1917:121. McDunnough 1938:169. Ferguson 1983:98.

Type locality: England ("Angliae rarissime"). Presumed to be a false type locality.

Microgonia resistaria Herrich-Schäffer, 1855, *Sammlung Aussereuropäischer Schmetterlinge*, p. 41, pl. [65], fig. 368.

Nematocampa resistaria, Walker 1860:147.

Type locality: not given.

Microgonia vestitaria Herrich-Schäffer, 1855, *ibidem*, pp. 63, 82, pl. [65], fig. 368.

Type locality: Brasil (considered to be an error; see below).

NOTE: Herrich-Schäffer proposed different species names, *resistaria* and *vestitaria*, on different pages of the same work in reference to the same figure. The names were published simultaneously, but *resistaria* has page priority. This synonymy was recognized by Guenée (1857, pt. 9:121), who applied the name *resistaria* and listed *vestitaria* as a junior synonym. Walker (1860:147) did likewise, but Guenée qualifies as the first reviser. Packard (1876:471) synonymized both under *N. filamentaria* Guenée but attributed *resistaria* to Walker, 1860, overlooking Herrich-Schäffer's prior publication. Although Guenée (1857), oblivious in this instance to the principle of priority, used the older name *resistaria* for what he thought was a South American variety of his new North American species, *N. filamentaria*, both Walker (1860) and Packard (1876) considered *resistaria* to be the North American species. The names *resistaria* and *vestitaria* of Herrich-Schäffer, *filamentaria* Guenée, and *limbata* Haworth continued to be treated as synonyms by most subsequent authors.

Although the only type locality mentioned by Herrich-Schäffer is Brasil (for *vestitaria*), his figure 368 clearly represents a male of the widespread North American species. I found no neotropical species or specimen that agrees with the figure and consider the locality to be an error. A similar error may be seen in figures 373 and 374 on the same plate (pl. [65]). The type locality for *Gnophos armataria* Herrich-Schäffer is given as Venezuela, although the specimens depicted are of the North American species treated in more recent literature as *Priocycla* or *Cepphis armataria* (Herrich-Schäffer).

Nematocampa filamentaria Guenée, 1857, *Hist. Nat. des Insectes, Species Général des Lépidoptères* 9:121; pl. 5, fig. 1; pl. 2, fig. 3 (larva). Packard 1876:471, pl. 11, fig. 46; pl. 13, figs. 8, 8a. Capps 1943:147. Forbes 1948:110. Ferguson 1954:321.

Type locality: Canada, by present lectotype designation.

NOTE: This species was described from one male and three female specimens from "Amérique septentrionale." The male and one female are in the United States National Museum (USNM); but the location of the second female, the syntype illustrated by Guenée (1857:pl. 5, fig. 1), has not been determined. Although this syntype appears to belong to the genus *Nematocampa*, it does not agree with any known species.

Ordinarily, one would choose the illustrated syntype as the lectotype, but because the source and identity of the specimen shown by Guenée are in doubt, I hereby designate as lectotype the male in the USNM, which bears the word "Canada" on a small, round label, as well as the usual Guenée and Oberthür labels and a Guenée type label. Although the right wings and abdomen are lost, the specimen clearly represents *resistaria*; all the more so because it is from a region where only that species is known to occur. The specimen reached the USNM with other Guenée types through the Oberthür and Barnes collections.

Nematocampa expunctaria Grote, 1872, *Canad. Entomol.* 4:101. Capps 1943:147. Ferguson 1983:98. **REVISED SYNONYMY**

Nematocampa limbata form *expunctaria*, McDunnough 1938:169.

Type locality: Alabama. [Holotype in Academy of Natural Sciences of Philadelphia.] *Ania limbaria* var. *chagnoni* Swett, 1913, *Canad. Entomol.* 45:76.

Type locality: Isle Ste. Therese, St. Johns Co., Quebec. [Holotype in Museum of Comparative Zoology, Harvard University (MCZ).]

NOTE: The name was based on one male of a melanic form of *N. resistaria*.

Nematocampa limbata orfordensis Cassino and Swett, 1922, *The Lepidopterist* 3:156. McDunnough 1938:169. Ferguson 1983:98. **REVISED SYNONYMY**

Type locality: Port Orford, Oregon. [Holotype male in MCZ.]

Eugonobapta brunneolineata Hulst, 1900, *J. New York Entomol. Soc.* 11:218. **REVISED SYNONYMY**

Ellopia brunneolineata, McDunnough 1938: 171

Nematocampa brunneolineata, Ferguson 1983:98 (as synonym of *expunctaria*)

Type locality: Hastings, Florida. [Holotype in American Museum of Natural History, New York.]

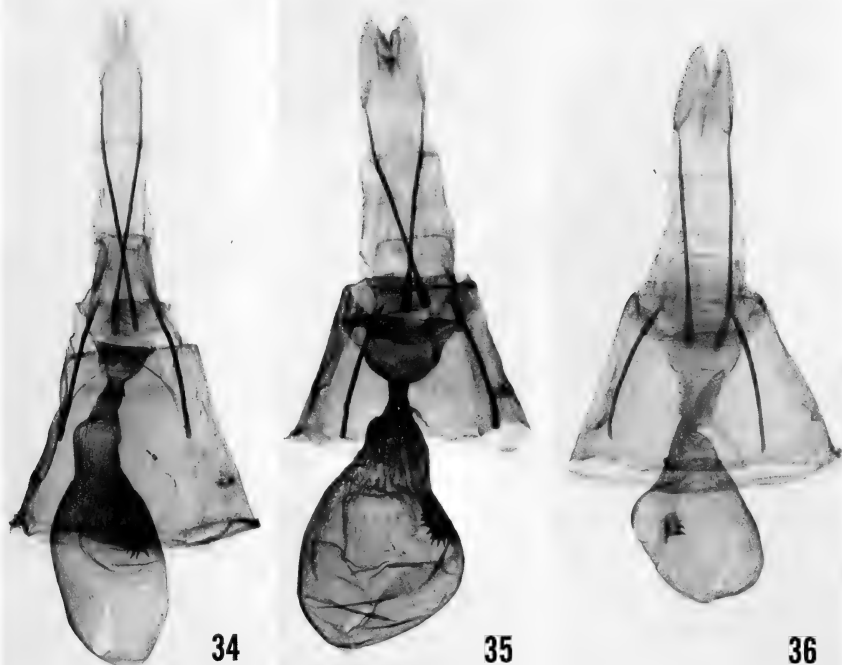
Diagnosis. This widespread nearctic species is distinguished by the pale whitish ground color of nearly all females (with rare exceptions) as compared to the more yellowish males; the swollen male hindtibia and the large size of the modified male hindtibial spur (Figs. 24, 25), which is swollen to three times the thickness of the other spurs; the combination of long, nearly straight prongs on the bifurcate juxta and the large coremata of the male genitalia (Fig. 28); and the combination of large, spiny signum but otherwise unsclerotized bursa copulatrix in the female genitalia (Fig. 34).

Further description. Both sexes with scales of front, antennae, palpi, and body light brown, legs and vertex somewhat paler.

Male (Figs. 1–13): Outer margin of forewing variable from rounded to angulate, hindwing usually rounded; ground color pale to deep yellow, with brown or purplish-brown markings well developed (Fig. 2) to obsolescent (Fig. 6) and geographically variable. Hindtibia much enlarged, apparently containing a large hair pencil that seems never to be fully extruded in museum specimens; hindtibia also with curiously modified, clavate, inner preapical spur twice as long as, and distally widened to at least three times as wide as outer preapical spur; modified spur longer than metatarsus. **Female** (Figs. 8–13): Outer margins of both wings angulate, that of forewing quite strongly so and concave between terminus of M_3 and apex. Ground color whitish or cream colored, with reddish-brown markings much less variable geographically than those of male (variation discussed below).

Undersides of both sexes paler and with markings less distinct than above. The reticulate nature of the wing pattern is more emphasized in females than in males because the longitudinal veins are more strongly outlined. Length of forewing: ♂♂, 10–14 mm; ♀♀, 12–14 mm (reared specimens may be smaller).

Male genitalia (Figs. 28, 29). Similar to those of *N. brehmeata* but with saccular lobe of valve more narrowed distally, prong of bifurcate juxta nearly straight and somewhat divergent, not incurved as in *brehmeata*, and with gnathos more produced distally; differ



FIGS. 34-36. Female genitalia. 34, *N. resistaria*, Okefenokee Swamp, Georgia. 35, *N. brehmeata*, Anderson Springs, Lake Co., California. 36, *N. baggettaria*, no locality (old specimen without data in U.S. National Museum).

obviously from those of *N. baggettaria* in having large coremata, a longer, slightly curved saccular (ventral) lobe on valve, and prongs on bifurcate juxta that are shorter than juxtal neck or base from which they arise.

Female genitalia (Fig. 34). Characterized by combination of large stellate signum, about three times wider than narrowest constriction of ductus bursae and often larger than that of *brehmeata* (specimen illustrated is an exception); an ovoid corpus bursae, twice as long as wide and with little sclerotization of its surface; and an ostial funnel whose widest dimension is considerably less than width of seventh segment at that point. By comparison, *N. brehmeata* (Fig. 35) has a wider ostial funnel, nearly as wide as the segment; more sclerotization on corpus bursae between signum and ductus bursae; and smaller signum only twice as wide as ductus bursae. *Nematocampa baggettaria* (Fig. 36) has an almost globular corpus bursae, and small, differently shaped signum hardly wider than narrowest constriction of ductus bursae.

Early stages. The peculiar larva of *N. resistaria*, which has been given the common name of "the filament bearer," was described and illustrated many times (e.g., Guenée 1857:pl. 2, fig. 3; Packard 1876:pl. 13, fig. 8; Peterson 1948:L56F; Furniss & Carolin 1977: fig. 122; Stehr 1987:504, fig. 26.281; Ives & Wong 1988:20, fig. G, p. 142, fig. E). Guenée's illustration was copied from a John Abbot drawing, probably of a specimen from Georgia; Packard's was a drawing of a larva from Salem, Mass.; Furniss and Carolin's was from the western U.S.; and Ives and Wong's were from the prairie provinces of Canada. These illustrations show considerable variation. Mosher (1917:41-43, fig. 2E, H) concentrated mainly on the pupa and illustrated it, but she also briefly described the larva.

The following is a description of the mature larva based mainly on photographs from T. L. McCabe of larvae from Pinebush, Albany County, New York, reared on *Quercus ilicifolia* (Fagaceae). Body cylindrical, of medium to somewhat stout form, with two unequal pairs of slender, tapered, fleshy, dorsal filaments arising from near the posterior margins of segments A2 and A3, the anterior pair being the longer and, when extended, nearly equal to the combined lengths of the first four body segments. Filaments somewhat extensile, straight when extended, bent and curled at the tips when retracted; pale basally, shading to dark purplish brown distally, but conspicuously white tipped, and with their surfaces appearing minutely tuberculate or pubescent. Correspondingly situated, brown, knoblike prominences on A1, each with a strong apical seta, and between these and the filaments of A2, two pairs of smaller, wartlike humps on A2, the anterior pair whitish, the following pair smaller and brown. Segment A8 somewhat elevated and pointed dorsally, after which the dorsum slopes downward abruptly toward the posterior edge of the anal plate. Head light rust red, marbled with pale tan to pinkish brown. Body variegated light and dark brown, the pale ground color often with a pinkish or purplish tint, although thoracic segments are dark brown and A1–2 partly yellowish brown. Dorsum from first pair of filaments to anal plate mostly dark brown, flanked by a gray to brown subdorsal stripe. Superimposed upon this are two or three dark-brown, oblique, abdominal bands that arise in the dorsal region and incline gradually downward and forward to just above lateral fold where they terminate in vague, elongate, diamond-shaped or fusiform, brown patches. Venter with a confused pattern of mainly rust-brown shading on a paler ground. Thoracic legs dark brown; prolegs mottled brown with whitish anterior edging on anterior proleg continuous with whitish posterior border of anal plate in one larva but not the other.

Ives and Wong (1988) published two colored photographs, one showing the filaments curled and the other showing them straight. Their illustrations also show a variable and complex pattern involving an irregular, continuous whitish lateral stripe on the head and first two thoracic segments, and oblique whitish lateral stripes on segments A6 to A8, the last running down the lateral side of the proleg. These features vary somewhat from those of the New York larvae described above. *Nematocampa resistaria* feeds on plants of at least 20 families. Prentice et al. (1963:489) listed the following as hosts (number of collections in parentheses): *Pseudotsuga menziesii* (Mirb.) Franco. (242); *Tsuga heterophylla* (Rafn.) Sarg. (220); *Abies balsamea* (L.) Miller (Pinaceae) (66); *Salix* spp. (Salicaceae) (20); *Picea glauca* (Moench) Voss (Pinaceae) (18); *Betula papyrifera* Marsh. (Betulaceae) (14); *Larix laricina* (DuRoi) K. Koch (Pinaceae) (12); *Thuja plicata* D. Don (Cupressaceae) (12); *Picea engelmannii* Parry (Pinaceae) (11); *Ulmus americana* L. (Ulmaceae) (8); *Larix occidentalis* Nutt. (6); *Pinus monticola* Dougl. (Pinaceae) (5); *Fraxinus americana* L. (Oleaceae) (5); and *Acer rubrum* L. (Aceraceae) (5); *Tilia americana* L. (Tiliaceae) (4); *Abies lasiocarpa* (Hook.) Nutt. (Pinaceae) (3); *Ostrya virginiana* (Mill.) K. Koch (Betulaceae) (2); *Acer negundo* L. (Aceraceae) (2); *Abies grandis* (Dougl. Lind.) (Pinaceae) (2); and *Alnus rubra* Bong. (Betulaceae) (2); Prentice et al. list 10 other host plants with only one collection for each, but only two additional plant families are represented, Rosaceae (*Prunus virginiana* L.) and Fagaceae (*Quercus macrocarpa* Michx.). The above records probably are biased in a way that reflects more thorough sampling of economically important trees and little attention to shrubs.

The compilation of host information by Tietz (1972) gives references to 25 food plants, of which the following are plants of genera not included above: *Aesculus hippocastanum* L. (Hippocastanaceae); *Carya* sp. (Juglandaceae); *Castanea dentata* (Marsh.) Borkh. (Fagaceae); *Corylus* sp. (Betulaceae); *Crataegus* sp.; *Pyrus ioensis* (Wood) Bailey; *Pyrus malus* L.; *Rosa* sp.; *Rubus allegheniensis* Porter; *Rubus idaeus* L. var. *strigosus* (Michx.) Maxim.; *Fragaria chiloensis* (L.) (all Rosaceae); *Humulus lupulus* L. (Moraceae); *Ribes americanum* Mill.; *Ribes lacustre* (Pers.) Poir.; *Ribes sativum* Syme (Saxifragaceae); *Robinia Pseudo-Acacia* L. (Fabaceae); and *Sedum* sp. (Crassulaceae). It was also reared from *Abies lasiocarpa* (Hook.) Nutt. (Pinaceae) at Bonner, Montana (U.S. Forest Service); *Liquidambar styraciflua* L. (Hamamelidaceae) (Kimball, 1965:186); *Myrica cerifera* L. (Myricaceae) (by D. Baggett, in USNM); *Myrica gale* L. (USNM); "sweet fern" [*Myrica asplenifolia* L.] (Mosher, 1917:43); *Quercus ilicifolia* Wangerh. (Fagaceae) (T. L. McCabe

pers. comm.); *Vaccinium arboreum* Marsh. (Ericaceae) (T. S. Dickel pers. comm.); *Ceanothus velutinus* (Rhamnaceae) in Idaho (U.S. Forest Service); *Amelanchier* and *Crataegus* spp. (Rosaceae) (L. R. Rupert; pers. comm. reported by the author, 1954:321); cherry (USNM); and *Gleditsia triacanthos* L. (Fabaceae) (reared by the author).

Distribution. *Nematocampa resistaria* occurs across southern Canada from Nova Scotia to Vancouver Island, B.C., southward at least to Hernando Co., Florida, Mississippi, southern Louisiana, Harris, Jackson, Colorado, and Blanco counties, Texas, and in the West at least to Morgan Co., Colorado, Sanpete and Wasatch counties, Utah, and Josephine Co., Oregon. In mountainous or semi-arid regions it is a species of low elevations and riparian habitats. It is replaced in California by *N. brehmeata*.

Flight period. The species is single brooded in Canada and most of the northern U.S., flying mainly in July and August. It becomes double brooded in the middle states, emerging in May and again in late July (e.g., in Maryland), but it seems to be no more than double brooded in the South. Thirty specimens in the USNM from South Carolina, Georgia, northern Florida, and Texas were all collected in April and May. In Louisiana and Mississippi it was collected in April, May, June, and July, based on many records from year-round light-trapping (V. A. Brou and B. Mather collections). The flight period in the Northwest is also mainly in July and August, rarely in June, but with a few September and early October records for western Oregon.

Geographical variation. *Nematocampa resistaria* has two main geographical variants that were named as species or subspecies: *N. expunctaria* (= *brunneolineata*) in the Southeast, and subspecies *orfordensis* in the Pacific Northwest. Grote (1872, 1882), Capps (1943:147), and the present author (1983:98) regarded *expunctaria* as a distinct species in which the wing pattern of the male is reduced to little more than the antemedial and postmedial lines (Figs. 6, 7). Females remain unchanged. Capps, knowing only the type of *expunctaria*, further described what he thought were differences in the genitalia. A reevaluation of more and better material now indicates that *expunctaria* is the same species as *resistaria*, at best a weak subspecies occupying a narrow coastal zone from South Carolina to northern Florida and westward through southern Louisiana to Texas. Intermediate forms of every degree may be found. Where the range of the species continues westward into eastern Texas, the moths revert to the more normal, well-marked form of *resistaria*. The differences in genitalia mentioned by Capps prove to be of no consequence when more than one specimen is examined.

The form described as *orfordensis* is localized and possibly related to the cool maritime climate of coastal Oregon, Washington, and Vancouver Island. It is as large as *N. brehmeata* (wing length: ♂♂, 13–14 mm; ♀♀, 15–16 mm) and sometimes, like that species, a deep shade of yellow. A size gradient is apparent between populations of the coastal region and the interior, those from eastern Oregon and Washington hardly differing from eastern specimens. Again, it is a poorly defined subspecies. However, one unusual feature of *orfordensis* is the occasional occurrence of yellow females colored like males (Fig. 12). Three of these in the USNM were collected near Elsie, Clatsop Co., Oregon on 5, 6 September 1963, 1968, and 1969. It is not a seasonal form because normal females with whitish ground color were collected with them. These are the only yellow females of *N. resistaria* that I have seen, although *N. brehmeata* always has yellow females.

Material examined. 244 adults, 7 genitalia slides.

Nematocampa brehmeata (Grossbeck) (Figs. 14–18, 26, 32, 33, 35)

Ania brehmeata Grossbeck, 1907, Trans. Amer. Entomol. Soc. 33:343.

Nematocampa brehmeata, Barnes and McDunnough 1917:121. McDunnough 1938:169. Ferguson 1983:98.

Type locality: Cazadero, Sonoma County, California. [Holotype in AMNH.]

Diagnosis. This is a Californian species in which both sexes are yellow, showing somewhat of a reversal of the sexual dimorphism of *resistaria*

because the females are often a deeper yellow than the males. The dark markings of the outer third of both wings in males are more broken up by encroachments of pale ground color and in females are lacking entirely. These yellow females, without dark submarginal markings, are very different in appearance from most females of *resistaria*. Diagnostic differences in the hindtibial spurs were noted in the key. In the male genitalia, the prongs of the bifurcate juxta are incurved distally, not straight. This species occurs in northern and central California west of the Sierra Nevada. It appears to be the only species of *Nematocampa* in that area, although *resistaria* occurs in nearby Oregon.

Further description. Body, head, antennae, and legs similar to those of *resistaria* except that modified hindtibial spur of male is more slender, distally swollen to not more than twice thickness of the other preapical spur, and slightly shorter than metatarsus. Wing shape and pattern similar to those of *resistaria* except that the dark, purplish-brown shading in outer third of wings in males tends to appear reduced, narrowed, or otherwise broken up, usually faded, and further reduced or lost on the hindwing. Dark shading of outer third of wings lost entirely in the four females examined. Ground color varies from light yellow to intense orange yellow in both sexes, but males are mostly light (9 of 11), and females may more often be deep yellow (2 of 4). Length of forewing: ♂♂, 12–14 mm; ♀♀, 13–14 mm.

Male genitalia (Figs. 32, 33). Differ from those of *resistaria* in slightly wider saccular lobe of valve; shorter coremata, only about half as long; narrower overall shape of juxta, with its two bowed prongs diverging basally but curving toward each other distally; and two free sclerites laterad of base of juxtal prongs thicker, and also bowed, not straight like those of *resistaria*.

Female genitalia (Fig. 35). Ostial funnel very large, almost as wide across opening as width of seventh segment at that point; about twice as large as ostial funnel of *resistaria*. Bursa copulatrix quite heavily sclerotized in zone between signum and ductus bursae; integument in this area pleated or rugose in both species, but not sclerotized in *resistaria*. Ovipositor wider and less elongated than that of *resistaria*, the lobes (papillae anales) being shorter than ostial funnel is wide (longer than width of funnel in *resistaria*).

Early stages. Unknown.

Distribution. I saw specimens from the following localities in California: Santa Cruz, Santa Cruz Co.; Los Gatos, Santa Clara Co.; Lucas Valley, Marin Co.; San Antonio Creek, Sonoma Co.; Napa, Napa Co.; Lucerne and Anderson Springs, Cobb. Mt., Lake Co.; Michigan Bluff, Placer Co.; Nelson Creek and Mohawk, Plumas Co.; Laytonville, Mendocino Co.; Oroville, Butte Co.; Hat Creek, Shasta Co.; Mt. Shasta (city), Siskiyou Co., and Gasquet, Del Norte Co. I collected three males of this species in a riparian habitat on the outskirts of the town of Mt. Shasta, on the road to Lake Shasta. The site was in a moist stream bottom with abundant willows, dogwood, and alder, mixed conifers nearby, and a pond fringed with *Typha* marsh.

Flight period. 20 June–27 August.

Geographical variation. Compared to those from elsewhere, three males from Mt. Shasta are smaller (wing length: 12–13 mm), slightly paler yellow, and with all dark markings intensified, although specimens from Shasta and Del Norte counties are the usual orange-yellow and more nearly normal in size and markings. The Mt. Shasta specimens could be mistaken for *N. resistaria*, but in pattern and structure they are *brehmeata*.

Material examined. Thirty-five adults, 5 genitalia slides.

Remarks. The distinction between *N. brehmeata* and *resistaria* may not always be as clear as I have indicated, because a few specimens that appear intermediate have been taken near the contact zone. Two males from Mt. Shasta (Fig. 14) almost have the markings of *resistaria*, and the male from McMinnville, Oregon, whose genitalia are shown in Fig.

28, resembles a deep-yellow male of *brehmeata*, although its juxta is clearly that of *resistaria*. Also, the only truly yellow females of *resistaria* (Fig. 12) are from Oregon, but they are otherwise consistent with *resistaria*, not *brehmeata*.

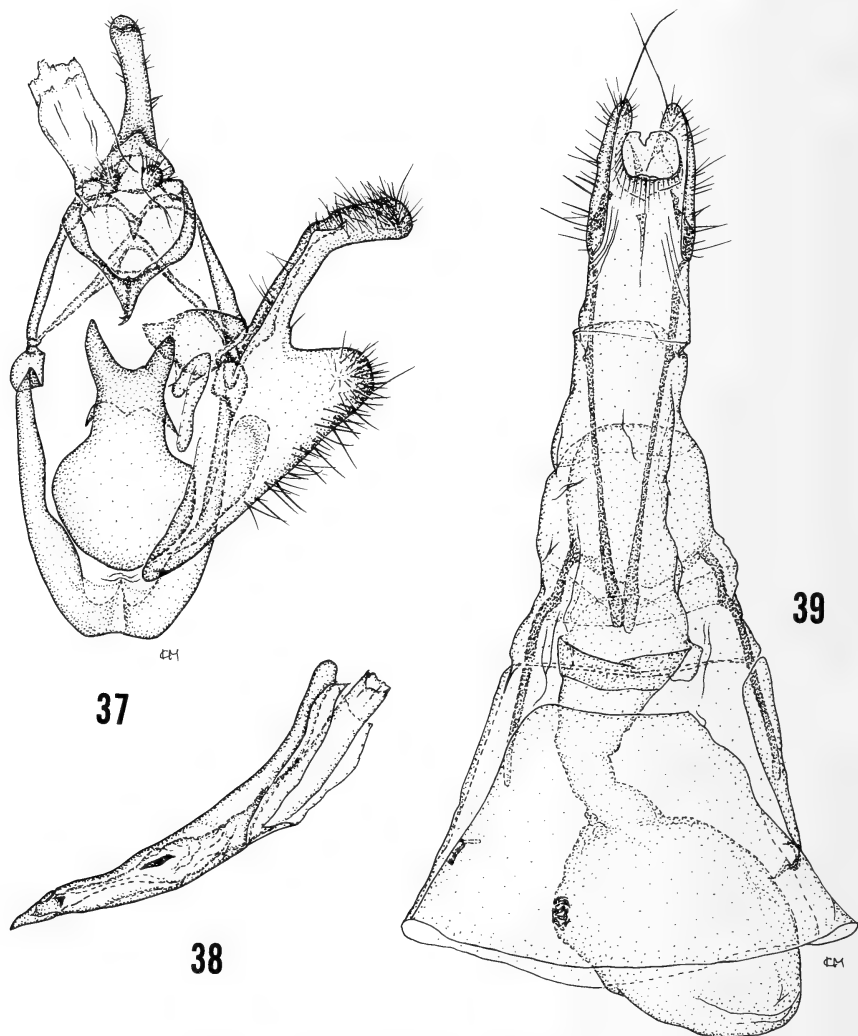
***Nematocampa baggettaria* Ferguson, n. sp.**

(Figs. 19–23, 27, 30, 31, 36, 37–39)

Diagnosis. This is the smallest and most distinct of the nearctic species, with the wing margins rounded, not angulate, wings mostly orange brown but with dark, purplish-brown shading in most of the outer third in females. The pattern is simplified, with two regular lines on the forewing, one on the hindwing, and almost no reticulation of lighter areas in either sex. It is the only species of *Nematocampa* in the U.S. without a swollen, clavate, hindtibial spur. The species is known from northern Florida and the central Gulf Coast region, and there is one record from Lumberton, North Carolina.

Further description. Head, antennae, and legs similar to those of *resistaria* except that the male hindtibia is not swollen and does not bear a specialized, large, clavate spur; all spurs are small and normal. Front in both sexes light yellowish brown, variably sprinkled with bright red-brown scales or with a diffuse red-brown border on each side. **Male** (Figs. 19–21): outer margin of wings rounded like those of southern *resistaria* or more so, and with apex less acute; wings almost uniformly ochreous orange brown, or variably tinged with purplish in outer third; forewing with antemedial a thin, dark, regular, convex line; postmedial line similar, curved subparallel to outer margin or nearly straight; hindwing with slightly curved postmedial line bisecting wing nearly in middle; small, rounded, dark discal dot on each wing; fringes dusky; wings faintly dusted with a few dark scales but without reticulation or any sign of a median band in median space. Underside darker, with markings reduced, although postmedial of hindwing may be closely preceded for most of its length by a faint, thinner, subparallel line. Spring brood (April) specimens with tendency to be slightly larger and paler than summer (June–August) specimens. Length of forewing: holotype, 8 mm; other ♂♂, 7–8 mm. **Female** (Figs. 22, 23): Apex of forewing somewhat produced but with outer margins rounded like those of male, unlike females of other species. Ochreous orange-brown ground color of wings dusted with reddish-brown scales that outline veins of median space in some specimens, giving a suggestion of reticulate pattern seen in pale wing areas of other species. Forewing with antemedial line thicker than that of male and purplish; postmedial line curved or nearly straight, blackish, commonly indented at cubital fold; postmedial of hindwing slightly curved to nearly straight, bisecting wing near middle. Discal spots small but prominent. Outer third of both wings dark purplish brown except for orange-yellow patch toward apex of forewing and variable indications of same color in form of a diffuse, mesial, transverse band in outer third of hindwing; fringes concolorous. Underside similarly marked but with lines thickened and diffuse, and all paler areas more or less suffused with gray or purplish brown. Little seasonal variation apparent. Length of forewing: 7–9 mm.

Male genitalia (Figs. 30, 31, 37, 38). Similar in general form to those of *N. resistaria* and *brehmeata* but with two conspicuous differences. Long, hairy coremata that arise near bases of saccular lobes in other species all but absent (vestiges remain), and prongs of bifurcate juxta are short in *baggettaria*. Prongs shorter than paired, longitudinally parallel sclerites lying off to each side of “neck” of juxta, whereas in *resistaria* prongs are much longer than these sclerites. Overall, genitalia smaller and more delicate, saccular lobe less produced, and vesica of aedeagus with smaller cornutus. Two specimens are illustrated to show variation. The prongs of the bifurcate juxta are asymmetrical in Fig.



FIGS. 37–39. Genitalia of *N. baggettaria*. 37, ♂, Abita Springs, Louisiana. 38, Aedeagus of same specimen. 39, ♀, Abita Springs, Louisiana.

37, which is probably not normal; and the aedeagus of the other specimen (Fig. 31) has a knoblike process on its proximal end, also abnormal.

Female genitalia (Figs. 36, 39). Main difference in female is in signum, which is small and of the simpler, two-pointed type found in some neotropical species. Signa of *resistaria* and *brehmeata* differ in being large, round or ovate disks bearing small surface points and fringed marginally with many more sclerotized points, which form a dentate margin on the signum that is widest toward its anterior end. Two specimens are illustrated, with the bursa copulatrix differently oriented.

Types. Holotype: ♂, Torreya State Park, Liberty Co., Florida, H. D. Baggett; in U.S. National Museum of Natural History. Paratypes (19): Torreya State Park, Liberty Co.,

Florida, 17 July 1982 (1 ♂), H. D. Baggett; same locality and date (1 ♀), W. L. Adair; same locality, 4 July 1986, (1 ♂, 1 ♀); 27 June 1981 (1 ♂); 17 Aug. 1982 (1 ♀); 4 Sept. 1983 (1 ♀), H. D. Baggett. Eight mi N of Sumatra, Apalachicola Natl. Forest, Liberty Co., Florida, 10 May 1990 (1 ♀), 2 June 1990 (1 ♂), H. D. Baggett. Goose Pasture, Jefferson Co., Florida, 27 May 1989 (1 ♂), H. D. Baggett. Manatee Springs State Park, Levy Co., Florida, 16 July 1982 (1 ♀), H. D. Baggett. Cedar Key, Levy Co. (Hardwood Swamp, CR-347, 5.4 mi N Jct. SR-24), Florida, 27 June 1987 (1 ♀), T. M. and L. Neal. 4.2 mi NE of Abita Springs, St. Tammany Parish, Louisiana, 25 Apr. 1984 (1 ♂), 7 May 1983 (1 ♂), 14 May 1984 (1 ♀), 25 May 1984 (1 ♀), 23 June 1983 (1 ♀), 16 July 1983 (1 ♂), 29 Sept. 1983 (1 ♂), V. A. Brou. Lumberton, North Carolina (on Interstate 95, at light), 21 Aug. 1987 (1 ♀), R. Gilmore. Paratypes deposited in U.S. National Museum, the Florida State Collection at Gainesville, and in the private collections of H. D. Baggett, V. A. Brou, and others.

Early stages. Unknown.

Distribution. Seen only from the Apalachicola National Forest and Torreya State Park, Liberty Co., Goose Pasture, Jefferson Co., and Manatee Springs and Cedar Key, Levy Co., Florida; Abita Springs, St. Tammany Parish, Louisiana; and Lumberton [Robeson Co.], North Carolina.

Flight period. Collected every month from April to September.

Material examined. Twenty-six specimens.

Remarks. This species is named for H. D. (Dave) Baggett of Palatka, Florida, who first brought it to my attention and who collected about half of the specimens seen.

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GENERAL NOTES

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DIMORPHISM IN THE FEMALE OF *BATTUS ZETIDES* (PAPILIONIDAE) ON HISPANIOLA

Additional key words: endemism, Antilles, systematics, variation.

N. D. Riley (1975) recorded *Battus zetides* Munroe (Papilionidae) as poorly known; in fact, based on the few specimens then extant, he incorrectly illustrated the species as lacking tails. Subsequent reports indicate that *B. zetides* can be found in isolated enclaves of upland mesic broadleaf deciduous forest, occurring on both the north and south paleoislands of Hispaniola (Gali & Schwartz 1983, Schwartz 1989, Johnson & Matusik 1988). Both Riley (1975) and Schwartz (1989) report the sexes of *B. zetides* as alike on both wing surfaces, as typical of most *Battus* species (D'Abrera 1981).

In 1988, we detailed location and habitat of the remote "Las Abejas" forest, Parque Nacional Sierra de Bahoruco [sic] (Pedernales Province, Dominican Republic) (Johnson & Matusik 1988). This upland forest, visited by us each year from 1981–1991, harbored a prolific population of *B. zetides* (Gali & Schwartz 1983) but is now suffering severe deforestation (Johnson & Matusik 1988, Johnson 1989).

The purpose of this note is to document a striking dimorphic female form of *B. zetides* occurring at Las Abejas. Contrasting the "ochre-yellow" or "yellows and oranges" generally attributed to wingbands of *B. zetides* (Riley 1975, Schwartz 1989; Fig. 1A), bands in this new form are mostly white, occasionally mottled pale yellow in distal areas of cells M_3 to $1A + 2A$ (Fig. 1B). This whitened condition, extending the silverlike appearance of the ventral hindwings (Fig. 1B, right), creates an identification problem in the field because such individuals resemble no other papilionid species known from the neotropics. To our knowledge, striking dimorphism in females of *Battus* has not been previously reported.

Ten specimens of the whitened female form have been collected at Las Abejas since 1986 (Specimen Data below) but, because our collections of *B. zetides* have been widely disseminated in public and private collections since 1981, it is difficult to quantify frequency of occurrence. Although females of *B. zetides* are generally less vagile than males and seldom venture from the forest canopy, females are probably more readily collected at Las Abejas than at other Hispaniolan locales since, as reported before (Johnson & Matusik 1988), steep ravine edges surrounding "Lower Abejas" allow for fortuitous collecting of the bottomland canopy. No doubt this unique collecting situation accounts for discovery of the form, which probably occurs in all populations of the species. A reconstructed estimate of frequency, based simply on recollection of collecting conditions for *B. zetides* at Las Abejas on a "day to day" basis, suggests females (usually immediately released) constituted about 5% of our catch. With this in mind, the ten known specimens of the whitened female probably represented about 1% of the females taken by us at the site.

It is important to note the striking appearance of this female form in the field. Field sightings have figured importantly in the historical documentation of certain rare, or seldom-collected, Antillean butterflies (Schwartz 1989, Brown & Heineman 1972). Schwartz (1989) has noted the soaring flight of *B. zetides* and that the butterfly is seen much more often than collected. The peculiar whitened female form of *B. zetides* should be anticipated by collectors and not misconstrued in flight as possibly representing an unknown neotropical swallowtail.

Specimen data (numbers parenthetical). All "Las Abejas forest" [detailed above], D. Matusik collector: 1–9 August 1991 (6) David Matusik Collection (DMC), 30 July 1990 (1) American Museum of Natural History (AMNH) (Fig. 1B), 29 June 1989 (2) (DMC), 5 July 1986 (1) (DMC).



FIG. 1. *Battus zetides*. **A**, Typical female ("Lower Abejas," *sensu* Johnson & Matusik [1988], 31 July 1990, AMNH) upper surface left, under surface right. **B**, Whitened female form (same data, except 30 July 1990, AMNH) same views.

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THE AHRENHOLZ TECHNIQUE FOR ATTRACTING TROPICAL SKIPPERS (HESPERIIDAE)

Additional key words: Pyrrhopyginae, Pyrginae, Hesperinae, army ants, behavior.

Skippers (Hesperiidae) constitute a large component of tropical butterfly communities. In South America, sites in mature lowland tropical forest may contain several hundred species. Although some species, especially those favoring clearings and heavily disturbed forests, may be locally common, most forest skippers occur at low population densities, as is generally true for tropical butterflies (Ebert 1969). Their swift, erratic flight is difficult to follow, and oftentimes, they are extremely wary. Thus, collecting and photographing forest skippers is difficult.

Various methods overcome the problem of sampling species that are otherwise rare and wary. Some butterflies are attracted to traps baited with rotting animals, excrement, decaying fruit, or pheromones. Others seek mud or sweaty clothes, presumably attracted to the sodium chloride. Malaise and light traps also may sample otherwise scarce species, and colored pieces of cloth, paper, or plastic can be effective in drawing high-flying species to the ground. Some butterflies, such as Ithomiinae and Danainae, seek pyrrolizidine alkaloids, whether in the nectar of Asteraceae or in decaying heliotrope plants (Boraginaceae).

Most skippers are not attracted to bait traps, show no interest in colored rags or plastics, and generally are not collected in Malaise and light traps. Only a small percentage of skippers sip moisture at mud, and most of these are males. Flowering shrubs or trees, which are heavily frequented by both sexes, are very scarce or patchy in South American rain forests and usually occur 20-45 m above the ground in the canopy.

It has been observed repeatedly, however, that many hesperiid species visit fresh bird droppings in the interior of the forest (mostly upon leaves or the ground) or on rocks, stones, or sand on river banks. Further, a number of otherwise scarce skippers congregate in the neighborhood of army-ant (Formicidae: Ecitoninae) swarms in southeastern Peru (Lamas 1983), where they feed on antbird (Formicariidae) droppings. Taking advantage of these peculiar congregations, first described by Zikán (1929) for Brazilian skippers, we have collected some species that are poorly represented in collections. Unfortunately, the thick underbrush and wariness of these skippers still makes it difficult to approach them.

The purpose of this note is to report a new method, which we name the "Ahrenholz Technique," for attracting skippers in Neotropical rain forests. It was devised and successfully used by our good friend David Ahrenholz in Rondônia, Brazil and eastern Ecuador. After he described the method to us in 1990, we experimented with it at Pakitza, Manu National Park; at Tambopata, Tambopata-Candamo Reserved Zone; and at Pampas del Heath National Sanctuary, in southeastern Peru (see Erwin 1985, 1991, Lamas 1985, Lamas et al. 1991 for location and description of the two former sites). We summarize our observations and those of Ahrenholz.

The Ahrenholz Technique

We placed small (ca. 1 cm²), approximately square, pieces of toilet or tissue paper, wetted with saliva, on the undersides of exposed, broad leaves, or on cleared patches of ground. These pieces of paper have a rough resemblance to fresh bird droppings and attracted many species of skippers, Nymphalidae (*Caeruleptychia*, *Pyrrhogyra*, *Adelpha*, *Nessaea*, *Catonephele*, *Marpesia*, *Memphis*, *Heliconius*, *Forbesia*), Riodinidae (*Euselasia*, *Ancyluris*, *Thisbe*), and Pieridae (*Dismorphia*). Other insects, including small flies, wasps, and orthopterans, visited the paper too. We also placed similar pieces of wet paper on sand at river banks, where only skippers and a few flies were attracted. We experimented with white, sky blue, light green, and light pink colored pieces of paper, without perceiving any differences in attractiveness. The exact shape of the paper did not seem to matter much either.



FIG. 1. *Astraptes fuligator* (Walch) (Pyrginae), on right, and *Aides duma argyrina* Cowan (Hesperiinae), attracted using the Ahrenholz technique, at Fazenda Rancho Grande, Rondônia, Brazil. Photograph courtesy of D. Ahrenholz.

A skipper, on discovering a piece of paper, landed quickly upon it, extended its proboscis and probed the wet paper for several seconds to a few minutes (Fig. 1). It remained wary, but was relatively easy to approach because we placed the paper in an exposed site. If the butterfly was collected, we replaced the paper, which usually fell into the net or on the ground, and wetted it again because dry paper was less attractive to the skippers. Although butterflies investigated paper wetted with rain water, they flew off after extending their proboscides. Other liquids, such as urine and sweetened soft drinks, did not work as well as saliva. Inside the forest, the paper attracted butterflies even if no ants were present, although with less success. Along river banks, they were effective whenever skipper butterflies were in the area.

Although skippers may use olfactory and/or auditory cues generated by the ants, their prey, and/or the antbirds to find ant swarms, they appear to locate bird droppings, or their "mimics" (the pieces of paper) visually, as shown at the river banks, where no ant swarms have been observed.

We list the skipper genera collected at Pakitza and Tambopata in October 1991, and at Pampas del Heath in June 1992, using the Ahrenholz Technique: A) Inside the forest. Pyrrhopyginae: *Jemadia*; Pyrginae: *Phocides*, *Phanus*, *Udranomía*, *Epargyreus*, *Augiades*, *Aguna*, *Polythrix*, *Chrysoplectrum*, *Urbanus*, *Astraptes*, *Dyscophellus*, *Telemiades*, *Pachyneuria*, *Clito*, *Zera*, *Quadrus*, *Gindanes*, *Milanion*, *Anastrus*, *Antigonus*, *Aethilla* and *Achlyodes*; Hesperiinae: *Vidius*, *Vettius*, *Justinia*, *Ebusus*, *Tigasis*, *Thoon*, *Talides*, *Tistas*, *Carystus*, *Carystoides*, *Perichares*, *Orses*, *Lycas*, *Metron*, *Phemiades*, *Panoquina*, *Oxyntes*, *Niconiades*, *Aides*, *Saliana*, *Thracides*, *Aroma* and *Pyrrhopygop-*

sis. B) At river banks. Pyrrhopyginae: *Pyrrhopyge*, *Elbella*, and *Jemadia*; Pyrginae: *Phocides*, *Proteides*, *Epargyreus*, *Polygonus*, *Antigonus*, *Anastrus*, *Ebrietas*, *Camptopleura* and *Cycloglypha*; Hesperinae: *Metron*, *Lindra* and *Panoquina*.

We are grateful to Dave Ahrenholz for allowing us to report his innovative technique and results. We thank the staff at Pakitza, Tambopata, and Pampas del Heath for supporting our research. This note is contribution no. 51, Biological Diversity in Latin America (BIOLAT) Project, Smithsonian Institution, and contribution no. 712, Departamento de Zoologia, Universidade Federal do Paraná.

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OBITUARY



DONALD PAUL FRECHIN (1918-1991)

Don Frechin, a Charter Member of the Lepidopterists' Society and well-known Washington state entomologist, passed away on 10 December 1991, at the age of 73. Don was born in Garden City, Kansas, on 6 January 1918; he moved with his parents to Bremerton, Washington, when he was 9 months old. He was an avid bug collector throughout his boyhood in western Washington. Following in his father's footsteps, he began working at the Navy shipyards in Bremerton in 1940. He married Gudrun (Gudy) Loyland in 1942 and raised seven children. In 1959, he took a job with the Boeing Company near Seattle, commuting by ferry for five years across Puget Sound. In 1964 the family moved to their north Seattle residence at 1745 Northeast 102nd Street, where Don lived out his life.

Don was an active collector throughout his life and exchanged specimens and information with many members of the Society. He was an ardent general collector, picking up examples of virtually all orders that could be pinned. Among the Lepidoptera, his passions included butterflies and larger moths, especially tiger moths and hepialids. Rearing insects was one of his favorite pastimes—he always had livestock around of sundry swallowtails, saturniids, and arctiids. For a time, he was involved with handpairing and hybridization of arctiids. Later in life he focused his attentions on tiger beetles, amassing a collection of nearly 8000 specimens.

Anyone who knew Don could not help but be impressed by his enthusiasm for, and knowledge of, Washington's insect fauna. As a graduate student studying the biosystematics of ghost moths, I sought out Don after seeing many of his hepialid specimens in major collections. Upon contacting Don, I found him to be the most knowledgeable Lepidopterist in North America on the habits of this seldom encountered family of Lepidoptera. I will never forget the time he (at the age of 64) took me to a trail at Steven's Pass in the northern Cascades, where he thought I might see *Gazoryctra roseicaput*. It was a cool, blustery September evening, clouds had engulfed the entire pass reducing visibility to little more than 30 feet. By dusk, when the moths were supposed to fly, the

temperature had dropped to 48°F (=9°C). I was sure no moths would be on the wing in such weather and suggested to Don that our time would be better spent at a lower, warmer elevation . . . perhaps in a restaurant with beverages on tap. He smiled and countered with a "wait and see" look. Sure enough, the moths appeared, when and where Don suggested—they disappeared almost as quickly, just thirty minutes later.

The size and nature of Don's collection was ever-changing as he often traded or sold parts of it. Eugene Munroe, acting on behalf of the Canadian National Collection (CNC), purchased most of Don's moths in the late 1950's, including Edward C. Johnston's important collection which Don recently had acquired. In the mid-1980's, I purchased Don's synoptic collection of Washington state Macrolepidoptera; this collection of 700 specimens is housed at the University of Connecticut. More than 39,000 specimens remain at his home in Seattle; the bulk of these are 22,000 Coleoptera and 14,500 Lepidoptera (mostly papered or unspread).

At least two species and one genus of insects were named after Don. Munroe described the pyralids *Pogonogenys frechini* and the genus *Frechinia*. Sanford Leffler described the tiger beetle, *Cicindela bellissima frechini*, endemic to the Olympic Peninsula, after him.

Don is survived by his wife, six children, and four grandchildren. Part of his legacy will be the countless collections he made of Washington state invertebrates, especially from the biologically unique areas that he so often visited, such as the Rocky Prairie near Tenino, the Olympic Peninsula, and the arctic-alpine areas of the northern Cascades. His absence from the Society will be keenly felt.

DAVID L. WAGNER, *Department of Ecology and Evolutionary Biology, U-Box 43, University of Connecticut, Storrs, Connecticut 06269-3043.*

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The merit of a scientific journal depends on the quality of its reviewers as well as of its authors, but the former are usually unknown to readers. The *Journal* relied on the expertise of 68 reviewers last year to provide 93 evaluations of manuscripts. It is with much gratitude that the *Journal* acknowledges the services of the people listed below from whom manuscript reviews were received in 1992.

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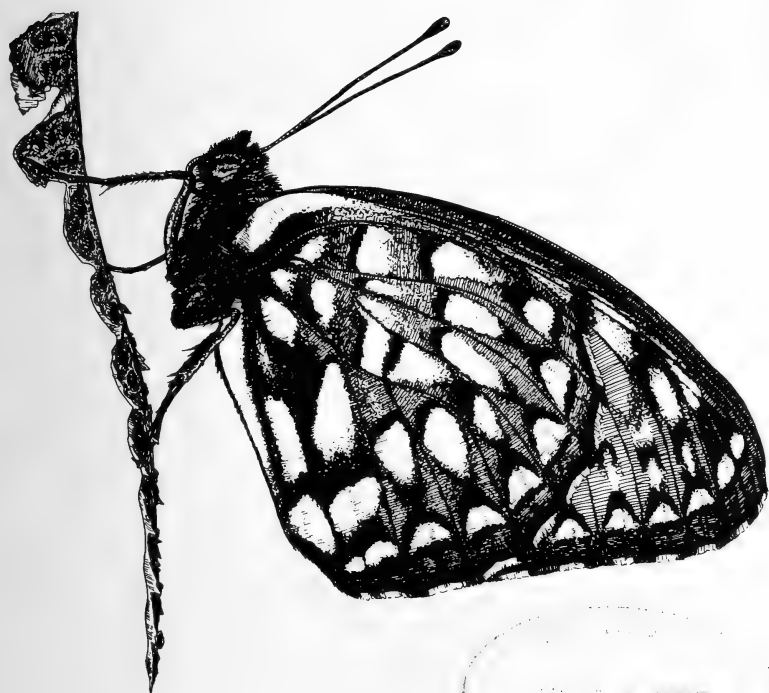
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Cover illustration: A silverspot butterfly (*Speyeria* sp.) resting beneath the leaf of a fern. Original drawing by Martie Clemons, Dudek and Associates, Inc., 605 Third Street, Encinitas, California 92024.

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BIOLOGY AND POPULATION DYNAMICS OF *PLACIDULA EURYANASSA*, A RELICT ITHOMIINE BUTTERFLY (NYMPHALIDAE: ITHOMIINAE)

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ABSTRACT. *Placidula euryanassa* is a primitive ithomiine restricted to the Atlantic coast of South America. Females lay eggs in clusters on *Brugmansia suaveolens* (Solanaceae). The larvae are gregarious, passing through five instars. Pupation occurs off the host plant; adults emerge after 8 to 14 days. In the laboratory the sex ratio is statistically equal to unity; in field captures the sex ratio is male biased. Individual mobility is low and the population size varies greatly during the year. Adults show a type II survival curve. Many biological features indicate that *Placidula* is relatively more r-selected than most Ithomiinae.

Additional key words: immatures, r-strategist, mark-recapture, Solanaceae.

Placidula euryanassa (Felder & Felder) is a member of the subfamily Ithomiinae. The systematic position of the species is uncertain (Brown 1987, Motta 1989). The genus *Placidula* is monotypic (Fox & Real 1971), with little or no morphological variation observed throughout its geographic distribution in southeastern Brazil and neighboring countries (D'Almeida 1938, Fox 1940, 1961, Biezanko 1960a, 1960b, Brown & Mielke 1967, Zikán & Zikán 1968, Fox & Real 1971, Brown 1979). Larvae of *Placidula euryanassa* have been found on the solanaceous plants *Brugmansia suaveolens* (Willd.) (= *Datura suaveolens* and *D. arborea*), *B. candida* Pers., *Datura stramonium* L., *D. metel* L., and *Cyphomandra betacea* Sendt. (D'Almeida 1938, Biezanko 1960a, 1960b, D'Araujo e Silva et al. 1968, Brown 1987, Drummond & Brown 1987). The last host plant may be incorrectly recorded (K. S. Brown pers. comm.).

The study of the biology of isolated genera of Ithomiinae is important for understanding relationships between this subfamily and its sister

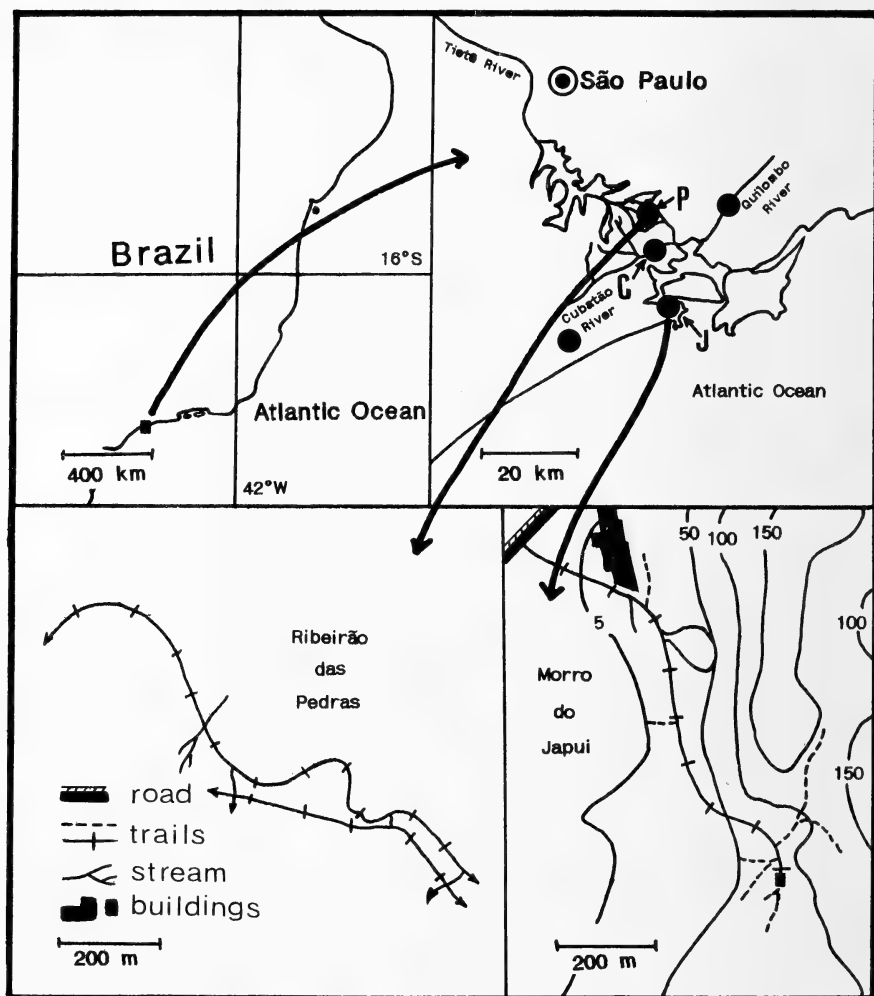


FIG. 1. Study areas in Southeast Brazil. In regional map (upper right), C = Vale do Rio Cubatão, J = Morro do Japuí, P = Ribeirão das Pedras. Two additional sampling sites are represented by solid circles.

group *Danainae*, and the evolution of these two groups (Gilbert & Ehrlich 1970, Young 1978a, Ackery & Vane-Wright 1984, Ackery 1987). Although *P. euryanassa* is considered a primitive ithomiine (Brown et al. 1991), it has many particular features that make it remarkable among the butterflies in this subfamily (the furry aspect of the larvae, the aggregative behavior of larvae, oviposition in large clusters, finely striated pupae). Previous workers have described some of these characteristics (D'Almeida 1938, Fox & Real 1971).

This paper reports on the early stages, larval host plant, habits, and population dynamics of *P. euryanassa*, and relates these features to those of other ithomiines.

STUDY SITES AND METHODS

Observations were made from 1 July 1988 to 30 December 1991, at five sites in São Paulo state, southeastern Brazil. One site is on the coastal plain (0–150 m elevation), three on lower mountain slopes (100–300 m elevation), and one on top of the Serra do Mar (750–800 m elevation), a mountain chain along the Atlantic coast (Fig. 1). Populations in the first and the last places, Morro do Japuí and Ribeirão das Pedras, respectively, were studied most intensively. The Ribeirão das Pedras site (46°31'W 23°49'S) supports montane rain forest (Ururahy et al. 1987) with an annual rainfall of over 4000 mm and an average annual temperature of 18°C (Setzer 1949). A large part of the area is old secondary forest, with a predominance of forest edge plants in the families Solanaceae, Melastomataceae, and Asteraceae. The Morro do Japuí site (46°24'W 23°59'S) supports submontane rain forest (Ururahy et al. 1987), with an annual rainfall near 2500 mm and an average annual temperature of 21°C (Setzer 1949, Prodesan 1969, Nimer 1972). A large part of this area is secondary forest, with a predominance of forest edge plants.

Eggs usually were collected in the field, but some were obtained in the laboratory from females. Three fertile females laid eggs in a glass jar covered with netting, with a leaf of the host plant and a cotton wad soaked in water/honey (3:1). When the jar was heated by a 100 W tungsten bulb at a distance of 20 cm (Freitas 1991), females increased their activity, and after 5–20 minutes began to oviposit. Larvae were reared on leaves of their natural host plant, in plastic boxes covered with netting. The boxes were cleaned daily.

Egg size is presented as height and width. The head capsule size of larvae is the distance between the most external ocelli (as in Freitas 1991). All measurements were made using a microscope with a calibrated micrometric ocular.

A mark-recapture census was conducted during March–December 1990 in Ribeirão das Pedras, and January–December 1991 in Morro do Japuí (Table 1). Visits to Ribeirão das Pedras were 1–3 times per week, and to Morro do Japuí 1–5 times per week. Butterflies were captured with an insect net, individually numbered on the underside of the forewings with a felt-tipped pen, and released at the point of capture. Several characteristics of each individual (sex, age, point of capture, source of nectar, and other activities) were recorded for later analysis.

TABLE 1. Mark-recapture studies of *Placidula euryanassa* in São Paulo, Brazil. Cap = total captured, Recap = total recaptured, L = maximum longevity, M = maximum movement.

Month	Cap		Recap		L	M	Multiple recaptures						
	♂	♀	♂	♀			1	2	3	4	5	6	7
1990: Ribeirão das Pedras													
Jan	0	0	0	0	—	—	—	—	—	—	—	—	—
Feb	0	0	0	0	—	—	—	—	—	—	—	—	—
Mar	2	1	0	0	—	—	—	—	—	—	—	—	—
Apr	24	30	2	1	13	50	3	—	—	—	—	—	—
May	6	12	0	0	—	—	—	—	—	—	—	—	—
Jun	13	10	1	0	6	10	1	—	—	—	—	—	—
Jul	0	2	0	0	—	—	—	—	—	—	—	—	—
Aug	0	1	0	0	—	—	—	—	—	—	—	—	—
Sep	0	0	0	0	—	—	—	—	—	—	—	—	—
Nov	0	0	0	0	—	—	—	—	—	—	—	—	—
Dec	0	2	0	0	—	—	—	—	—	—	—	—	—
Total	45	44	3	1	13	50	4	—	—	—	—	—	—
1991: Morro do Japuí													
Jan	0	0	0	0	—	—	—	—	—	—	—	—	—
Feb	0	0	0	0	—	—	—	—	—	—	—	—	—
Mar	0	0	0	0	—	—	—	—	—	—	—	—	—
Apr	1	1	0	0	—	—	—	—	—	—	—	—	—
May	45	22	10	2	8	50	11	1	—	—	—	—	—
Jun	20	7	7	2	8	100	7	1	1	—	—	—	—
Jul	139	70	33	18	43	270	36	11	3	1	—	—	—
Aug	75	53	26	22	18	200	31	13	3	1	—	—	—
Sep	158	143	90	88	30	100	81	45	27	15	4	3	3
Oct	1	1	0	0	—	—	—	—	—	—	—	—	—
Nov	1	2	0	0	—	—	—	—	—	—	—	—	—
Dec	1	0	0	0	—	—	—	—	—	—	—	—	—
Total	440	299	149	112	43	270	135	68	31	17	4	3	3

The "age" of individual butterflies was estimated by rating them in one of six categories based on wing wear (Ehrlich & Davidson 1960, Brussard & Ehrlich 1970, Ehrlich & Gilbert 1973, Brown et al. 1981). Time of residence in the population was estimated following Brussard et al. (1974), and survival curves follow Ehrlich and Gilbert (1973). The butterflies flew slow enough to be captured easily without damage.

The mark-recapture data were analyzed by the Jolly-Seber method for estimating population parameters (Southwood 1971). Males and females were analyzed separately.

Levels of flower visitation were recorded during the two years of population studies. A plant species was classified as highly visited if 50 individuals or more were observed feeding on its flowers, intermediate if 10 to 49 individuals were observed, and low if fewer than 10 individuals were observed on it during the two years of study.

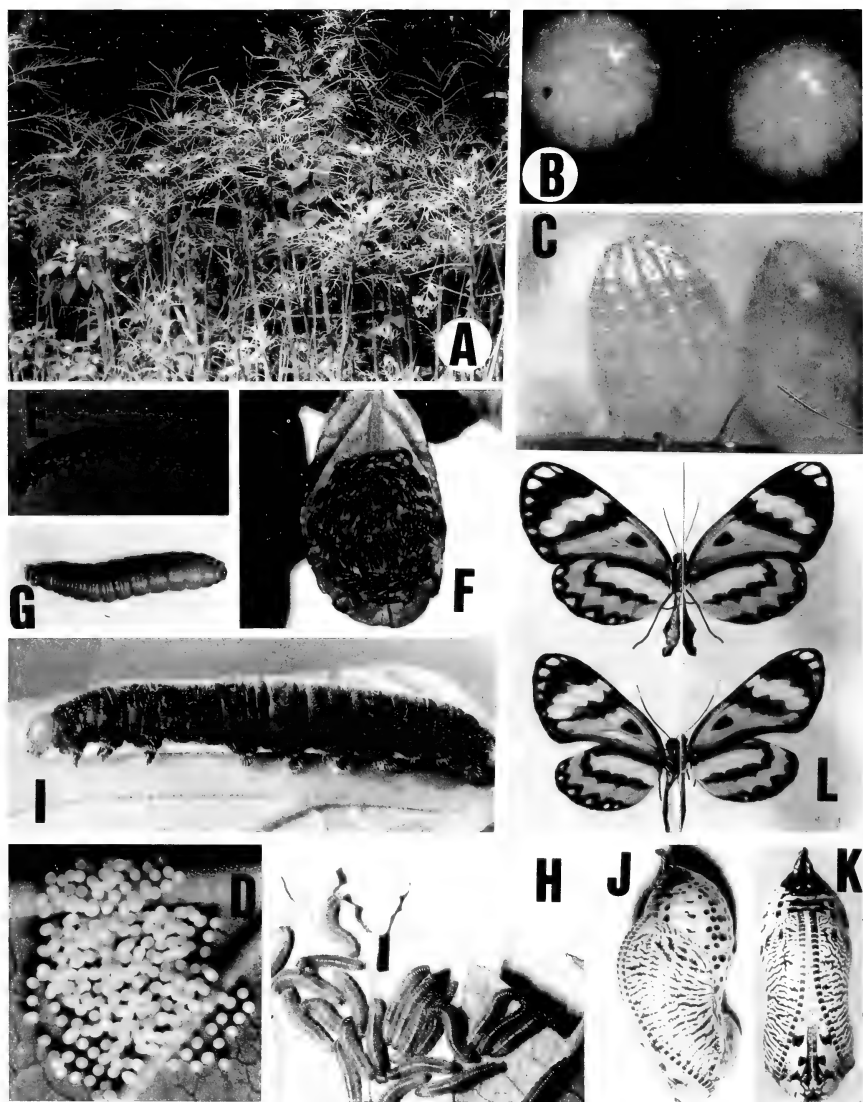


FIG. 2. Natural history of *Placidula euryanassa*. A, defoliated food plants (Ribeirão das Pedras); B, C, 2 eggs (dorsal, lateral); D, egg mass; E, first instar larva; F, group of second instar larvae; G, third instar; H, group of fourth instar larvae; I, fifth instar; J, K, pupa (lateral, ventral); L, adults (female above, undersides on left).

RESULTS

General Biology

Brugmansia suaveolens is the only host plant of *Placidula* in the study areas (Fig. 2A). Before ovipositing, the female usually flies around

the host plant and touches several leaves with its legs and antennae while hovering. After selecting a leaf, the female lands directly on the ventral surface and lays her eggs. Additionally, two egg groups were discovered on boards in contact with the food plant. Eggs were laid in tight clusters (Fig. 2B), generally near water or in very humid sites. On the coastal plain, egg rafts typically were found on leaves 10–100 cm above running water. In Ribeirão das Pedras, all host plants were at least 100 m away from water, but the humidity was very high with mist frequent. Egg rafts contained 107 to 307 eggs (\bar{x} = 212.5; SD = 71.3; n = 9).

After hatching, caterpillars eat part of the egg shell. The caterpillars are very sensitive to low humidity and die rapidly in drier environments. The larvae are gregarious in all stages, resting in compact groups on the lower surface of the leaves. In the fifth instar, however, they rest in groups on stems near the ground, climbing up only to feed on leaves. High nocturnal feeding activity of larvae was observed in the laboratory and on a garden plant, suggesting a pattern of nocturnal feeding and diurnal resting. The caterpillars eat all the leaf tissue, leaving only the larger veins. A single group of 200 larvae can defoliate an entire host plant (Fig. 2A); the larvae then descend to the ground to search for another plant, moving as a loose chain. On 29 July 1990, Ribeirão das Pedras was affected by a strong frost (-1°C), and many of the *B. suaveolens* on which larval groups were being followed, lost their leaves. Some larval clusters later were found in good condition on nearby plants, indicating that they could survive freezing temperatures.

When disturbed, caterpillars rear up and swing the anterior portion of their body, showing their red head. This is different from other Ithomiinae whose larvae often suspend themselves from silk threads (Young 1972). The J-shaped resting position, common in other Ithomiinae and Danainae (Brown & D'Almeida 1970, Young 1972, 1974a, 1974b, 1974c, 1978b, Ackery 1987), was not observed in the tightly gregarious larvae of *Placidula*.

Pupation usually occurs off the host plant in shaded protected places (under rocks, stems and wood boards) no more than 2 m above the ground. Adult eclosion takes place in the early morning with adults generally flying before midday.

Description of Early Stages

Egg (Figs. 2B, C, D): White, oblong, apex tapering to a slightly flattened acute angle, with 17 to 19 longitudinal ridges and 16 to 18 transverse ridges. Average height 1.0 mm (SD = 0.052, n = 21); average width 0.69 mm (SD = 0.076, n = 26), duration 8 to 10 days (for two ovipositions with 200 and 230 eggs obtained in laboratory). Descriptions

and photographs of the egg of *Placidula* have been presented previously by Motta (1989).

First instar larva (Fig. 2E): Translucent white with a dark brown head, becoming pale green after feeding (due to visible intestinal contents); maximum length 3 mm; average width of head capsule 0.44 mm (SD = 0.013, $n = 11$), duration always 5 days with synchronized molting ($n = 30$).

Second instar (Fig. 2F): Pale gray, head pale brown, dark intestinal contents evident; maximum length 5 mm; average width of head capsule 0.63 mm (SD = 0.023, $n = 12$); duration 5 days ($n = 25$).

Third instar (Fig. 2G): Pale gray, head reddish brown; maximum length 12 mm; average width of head capsule 1.0 mm (SD = 0.041, $n = 19$); duration 4 days ($n = 25$).

Fourth instar (Fig. 2H): Body black following ecdysis; dark gray with a "furry" aspect owing to many short bristles on the cuticle following feeding and growing; head red with black ocelli; maximum length 21 mm; average width of head capsule 1.5 mm (SD = 0.095, $n = 22$); duration 5 days, with totally synchronized molting ($n = 25$).

Fifth instar (Fig. 2I): Body black with a furry aspect; head red, ocelli black; maximum length 32 mm; average width of head capsule 2.30 mm (SD = 0.230, $n = 13$); mean duration 7.3 days (SD = 1.24, $n = 24$). When placed in pure methanol, the larva shows a striped color pattern similar to that found in danaines and primitive ithomiine butterflies (Ackery & Vane-Wright 1984, Brown 1987).

Prepupa: Assumes a "J" position, fixed on the substrate by the anal prolegs and abundant silk; body black but with a translucent aspect.

Pupa (Figs. 2J, K): Opaque, sometimes a little reflective, with many small black spots, stripes, and other markings; cremaster black; mean duration in autumn (11–23 May 1989) 10.4 days (SD = 0.50, $n = 50$), significantly shorter than in winter (1–16 August 1989), i.e., 13.9 days (SD = 0.21, $n = 22$) (Mann-Whitney test, following Brower & Zar 1984, $t = 6.723$, $P < 0.001$). Average length 1.49 cm (SD = 0.086, $n = 25$).

Descriptions of the adult (Fig. 2L) have been presented previously by Haensch (1909) (as *Ceratinia euryanassa*), D'Almeida (1938), and Fox and Real (1971). The sex ratio of adults obtained in the laboratory (42 males and 67 females from 3 broods) can be considered 1:1 (chi square test; $\chi^2 = 5.73$; $P > 0.05$; $df = 1$).

Adult Population Biology

Of 101 individuals of *P. euryanassa* marked at Ribeirão das Pedras, only four were recaptured. In contrast, 261 of the 739 individuals marked at Morro do Japuí later were recaptured at least once (Table

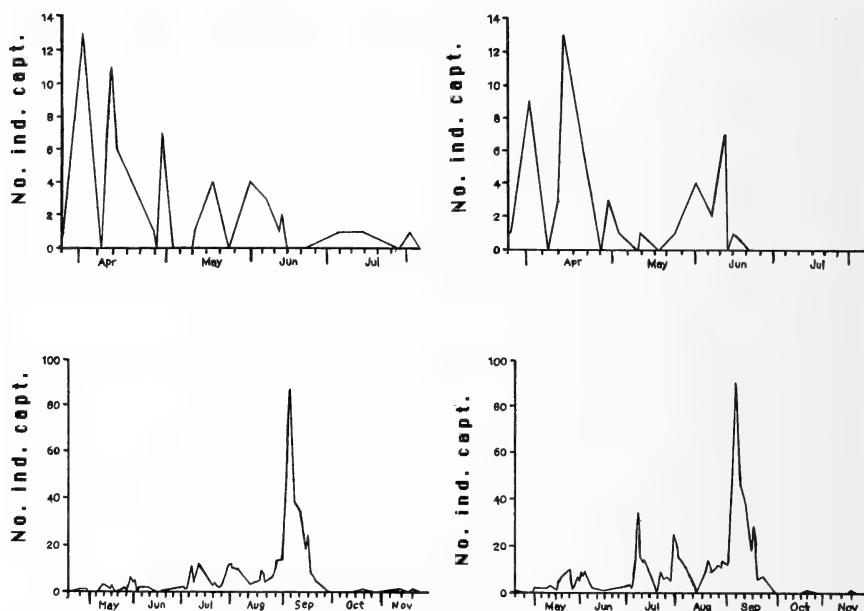


FIG. 3. Daily captures of *P. euryanassa* in Ribeirão das Pedras, 1990 (upper), and in the Morro do Japuí, 1991 (lower), females (left) and males (right). Divisions within months (horizontal axis) represent intervals of 5 days.

1). For this reason, most population parameters were calculated only for the Morro do Japuí population.

At Ribeirão das Pedras, adults were most abundant during April and May, diminishing later in June, and disappearing completely in August. The flight periods of males and females were similar. At Morro do Japuí the population size varied during the year and showed three distinct peaks: small in May, medium in July, and high in August and September. The population of adults diminished abruptly at the end of September, and very few individuals were marked in October, November, and December (Fig. 3). Few individuals of one peak were captured in the following one. The dynamics of the males and females were similar.

Population size was analyzed using the Jolly-Seber method for the three high recapture peaks. The results are presented in Fig. 4. For these three periods, the recaptures were shown to be random by fitting the actual data against a Poisson distribution with the chi-square test.

Sex Ratio

At Ribeirão das Pedras the numbers of males and females were approximately equal (46 males and 55 females marked; $\chi^2 = 1.2$; $P >$

0.20; $df = 1$), except in months with low captures (July and August). However, at Morro do Japuí the sex ratio could not be considered 1:1 (440 males and 299 females marked; $\chi^2 = 26.9$; $P < 0.001$; $df = 1$). Males were the dominant sex during the study year, except in months with low captures (April, October, and November) (Fig. 5). The proportion of recapture of males (33.9%) and females (37.5%) can be considered equal ($\chi^2 = 1.0$; $P > 0.20$; $df = 1$).

Vagility

At Ribeirão das Pedras the few individuals recaptured were at the same location as marked, and little information could be obtained (although two individuals were recaptured 15 days after marking). At Morro do Japuí the movement of adults was limited; the distance between point of release and recapture rarely exceeded 100 m. Of 261 recaptures, 125 males (83.9%) and 93 females (83.0%) were recaptured less than 100 m from the site of first capture, and 24 males (16.1%) and 19 females (16.9%) were recaptured 100–300 m away. The greatest distance was 300 m, although some individuals were followed for more than 100 m before being captured. The host plants at Morro do Japuí are concentrated in a single area 450 m from the most distant point of capture and 100 m from the nearest source of nectar. From 1988 to 1992, some individuals of *P. euryanassa* were collected in the city at least 1000 m away from any place considered suitable for maintenance of a colony. Seven of these were females and two were males. These data provide limited support for the hypothesis that females disperse widely while searching for places to lay eggs. A female transferred from the city to Morro do Japuí was captured in the same place as released, 20 days later.

Age Structure

The 6 initial age categories were grouped into 3: 1) new, including freshly emerged and new; 2) intermediate (the same); and 3) old, including old, very old, and tattered.

At Ribeirão das Pedras, the age structure of the *P. euryanassa* population was dominated by new individuals (only seven intermediate and one old were marked during the entire year). At Morro do Japuí, the age structure of *P. euryanassa* was unclear during the initial months of the study owing to the low number of individuals captured per day. Data from different days were not combined, however, because the age structure was easily observed in population peaks.

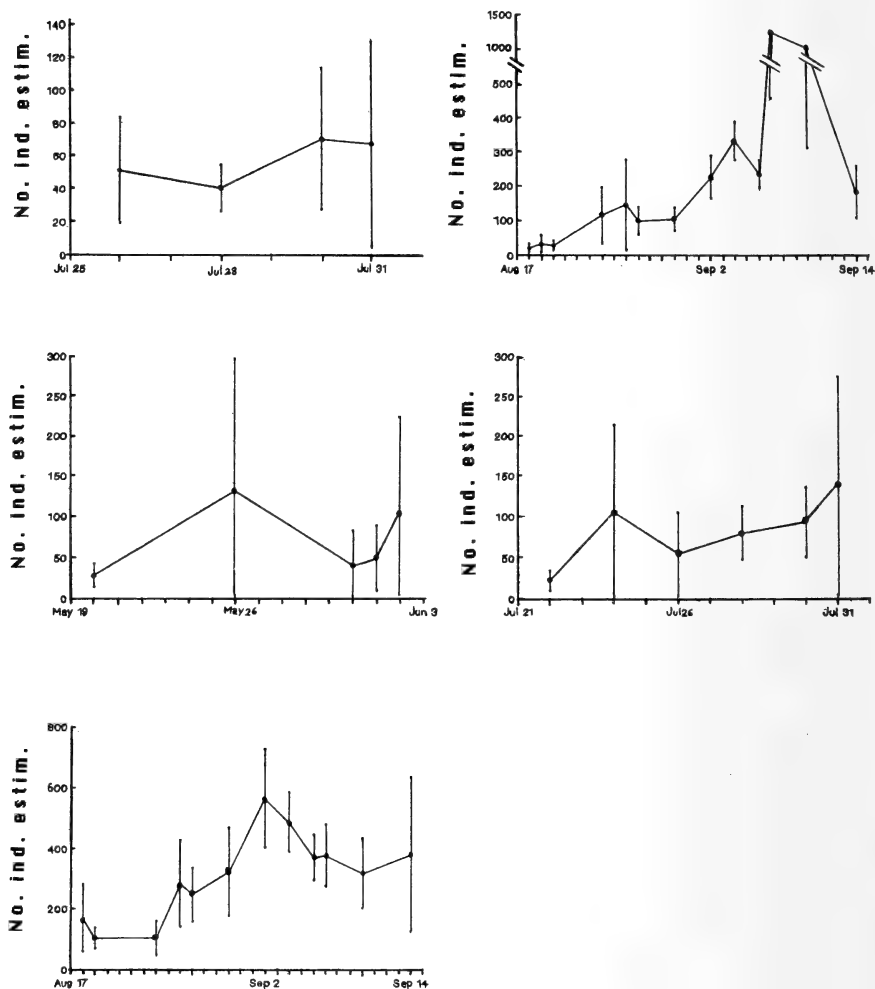


FIG. 4. Estimated population size (Jolly-Seber) for *P. euryanassa*, Morro do Japui, 1991. Females (top row, two peaks) and males (middle and bottom rows, three peaks).

In general, each population peak started with many new individuals. Later in the peak, intermediate individuals predominated, and at the end of the population peak, most individuals were scored as old, both males and females, especially in the August/September period (Fig. 6).

Time of Residence

Males have a residence time ($\bar{x} = 8.38$; $SD = 8.34$; $n = 149$) longer than females ($\bar{x} = 7.23$; $SD = 5.69$; $n = 112$) (Table 2). The survival curves of *P. euryanassa* are similar in males and females (type II), but

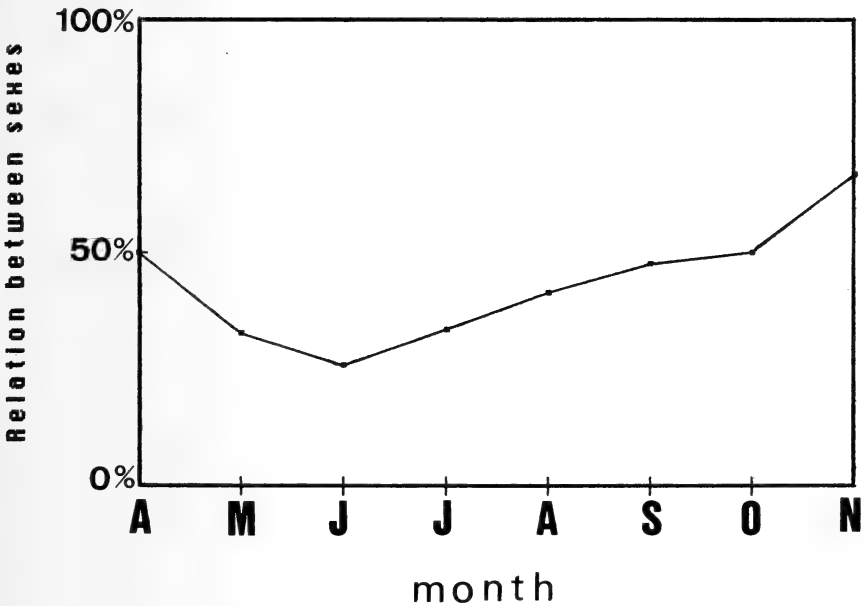
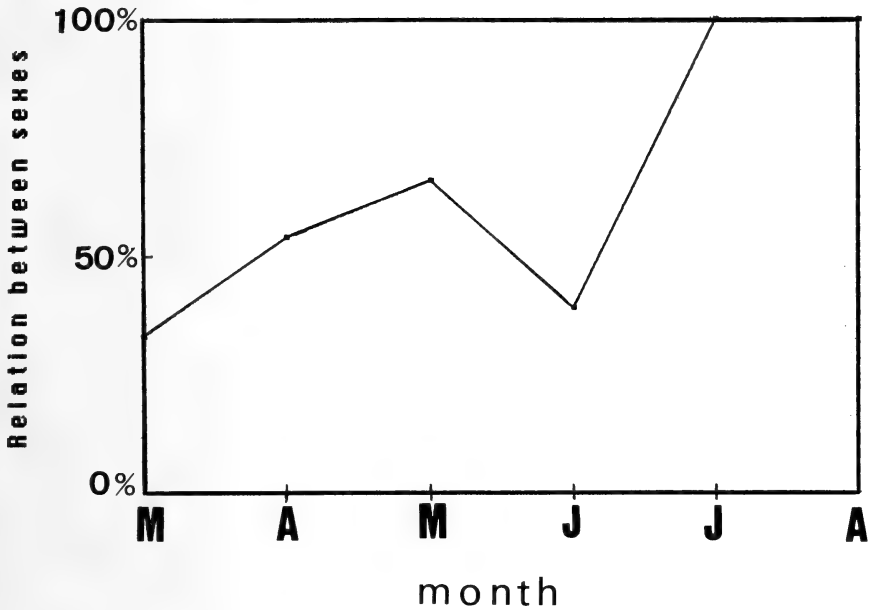


FIG. 5. Sex ratio for *P. euryanassa* marked in the Ribeirão das Pedras (1990, upper) and Morro do Japuí (1991, lower), as percent of ♀♀ in each day's captures.

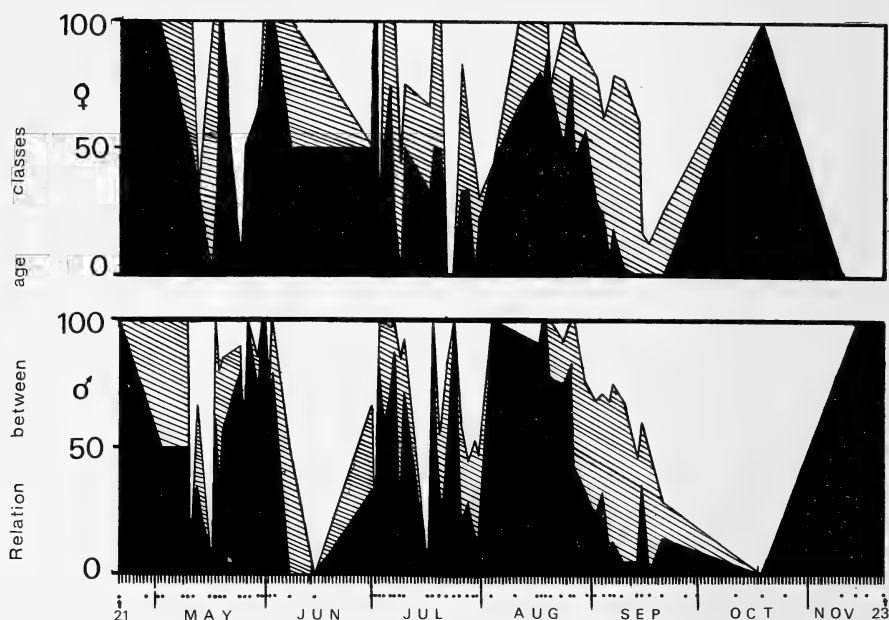


FIG. 6. Age structure of females (above) and males (below) of *P. euryanassa* in Morro do Japuí, April to November 1991: black = Fresh individuals, hatched = intermediate, white = old, as % of total on each day. Actual sampling days are indicated by points along the horizontal axes.

the survivorship of the latter is higher in individuals from 6 to 20 days of age (Fig. 7).

Adult Food Sources

Adults always were encountered near a nectar source. A few individuals were observed sucking broken stems of *Eupatorium punctu-*

TABLE 2. Permanence of marked *P. euryanassa*. Days elapsed between marking and last recapture represent the minimum permanence (MP) for each individual.

MP	Males	Females	Total
1-5	75	55	130
6-10	34	21	55
11-15	17	23	40
16-20	9	12	21
21-25	5	1	6
26-30	5	0	5
31-35	2	0	2
36-40	1	0	1
41-45	1	0	1
Total	149	112	261

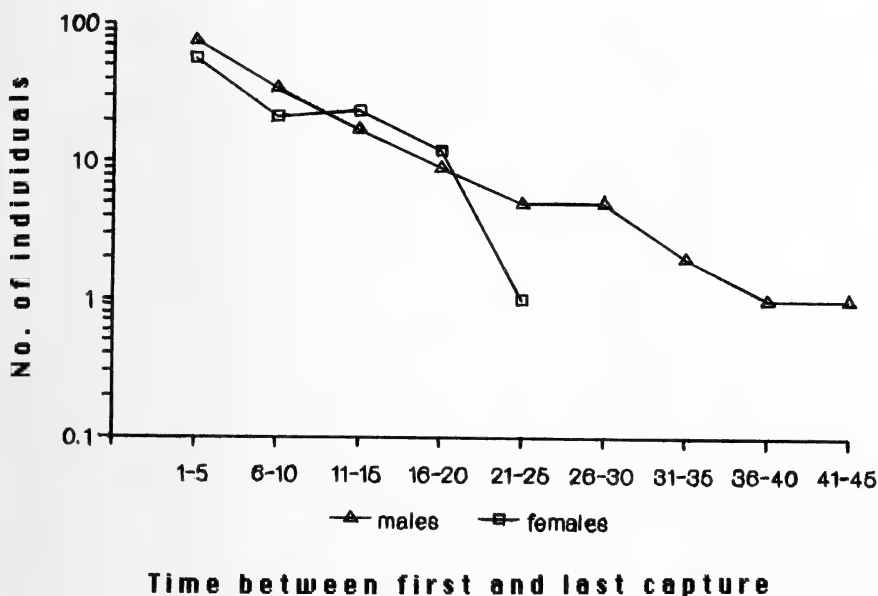


FIG. 7. Survivorship curves for *P. euryanassa*, Morro do Japuí, 1991 (following Ehrlich & Gilbert, 1973).

latum D.C. (Asteraceae) (three males), and leaves of *E. inulaefolium* H.B.K. (Asteraceae) (one male), perhaps attracted by the pyrrolizidine alkaloids contained in these plants (Brown 1985, 1987). Most flowers visited by *P. euryanassa* are in the Asteraceae, but the use of many other families was observed (Table 3).

Adult Behavior

Placidula euryanassa is a common species found in secondary forests. Adults frequently are found on Asteraceae flowers or near their host plants, flying slowly 1–5 m above the ground.

Where flowers were not present, adults were captured in flight; they typically flew below 3.5 m (reach of the net). Adults of *P. euryanassa* flew higher than other Ithomiinae present in the study areas [such as *Heterosais edessa* (Hewitson), *Pseudoscada erruca* (Hewitson), *Hypoleria adasa* (Hewitson) and *Hypothyris ninonia daeta* (Boisduval), that fly less than 2 m above the ground], being comparable only to *Dircenna dero celtina* Burmeister, *Melinaea ludovica paraiya* Reakirt, and *M. ethra ethra* (Godart) (species that fly above 5 m when not feeding).

Adults of *P. euryanassa* were observed resting in sunlight on cold days (14–16°C) during early morning (0800 h). These individuals generally were so sluggish that they could easily be captured by hand.

TABLE 3. Level of visitation of nectar sources by adults of *Placidula euryanassa*. *** = high, ** = intermediate, * = low.

Nectar source	Level
Asteraceae	
<i>Eupatorium gaudichaudianum</i> D.C.	***
<i>E. laevigatum</i> Lam.	***
<i>E. betonicaeforme</i> (D.C.) Baker	***
<i>E. inulaefolium</i> H.B.K.	**
<i>E. maximiliani</i> Schraeder	**
<i>E. punctulatum</i> D.C.	*
<i>Mikania lundiana</i> D.C.	**
<i>M. micrantha</i> H.B.K.	**
<i>M. lanuginosa</i> D.C.	**
<i>M. cordifolia</i> (L.F.) Willd	*
<i>M. hatschbachii</i> G. M. Barroso	*
<i>Mikania</i> sp.	**
<i>Vernonia scorpioides</i> (Lam.)	**
<i>V. lindbergii</i> Baker	***
<i>V. beyrichii</i> (Less.)	***
<i>V. condensata</i> Baker ¹	***
<i>Trixis antimenorrhoea</i> Mart. ex. Baker	***
<i>Senecio</i> sp.	***
<i>Alomia fastigiata</i> Benth.	***
<i>Adenostemma viscosum</i> Forst.	*
<i>Ageratum conyzoides</i> Linn.	*
<i>Emilia sonchifolia</i> D.C.	*
Rubiaceae	
<i>Mitracarpus hirtus</i> D.C.	**
<i>Borreria</i> sp.	**
Rosaceae	
<i>Rubus rosaefolius</i> Smith	**
Verbenaceae	
<i>Lantana camara</i> L.	*
Boraginaceae	
<i>Cordia verbenacea</i> D.C.	*
Lauraceae	
<i>Persea americana</i> Mill. ¹	***

¹ Introduced plants.

The few females observed ovipositing were always evaluated as intermediate ($n = 2$) or old ($n = 1$) in age class, and ovipositions in the laboratory were obtained only with females in these categories (i.e., 1 intermediate and 2 old; 4 new females did not oviposit).

DISCUSSION AND CONCLUSIONS

Biology of Immatures

Eggs laid in clusters and gregarious larvae are characteristic features of the biology of *P. euryanassa*. The habit of not eating the egg shell (or eating only a part) may be related to the proximity of the eggs of

siblings that could be eaten by mistake. Many Ithomiinae that lay eggs in clusters do not eat the egg shell, including members of the genus *Mechanitis* and *Hypothyris euclea laphria* (Doubleday) (pers. obs.). On the other hand, Ithomiinae that lay eggs singly usually eat the entire egg shell (Brown & D'Almeida 1970, Young 1974a, 1974b, 1974c, 1978a, 1978b, Muyschondt et al. 1976). The genus *Tellervo*, however, lays eggs singly and larvae eat only part of the egg shell (Ackery 1987).

The choice of oviposition sites can be related to climatic factors, especially weather and humidity, with eggs always near water except when atmospheric humidity is always at the saturation point (100%).

A "J" shaped resting position is observed in many larvae of Ithomiinae and Danainae, including *Tellervo* (Young 1972, 1974a, 1974b, 1974c, 1978b, Ackery 1987), but not in *Placidula*. The proximity of larvae when feeding or at rest can explain the inconvenience of this behavior. The "J" shape position is rare or absent in other gregarious Ithomiinae and also in young larvae of *Dircenna dero*, that rest along leaf veins (pers. obs.).

Among the Ithomiinae, the behavior of larvae resting in groups near the ground (or water) is known only in *Placidula*. The striped pattern of *P. euryanassa* larvae illuminated when placed in methanol and the corrugated cuticle, typical of late instars, are very similar to those of *Danaus*, *Lycorea*, *Ituna*, and primitive Ithomiinae, such as *Tithorea*, *Aeria*, *Elzunia*, and *Melinaea* (Gilbert & Ehrlich 1970, Muyschondt et al. 1976, Young 1978a, Brown 1987). These two features are considered as important indications of phylogenetic relationships between Ithomiinae and Danainae butterflies (Young 1978a, Gilbert & Ehrlich 1970). The furry aspect of late instar larvae occurs only in *Dircenna* and *Hyalenna* among other Ithomiinae (Young 1973, pers. obs.).

Larvae of *P. euryanassa* have been considered aposematic in color pattern and behavior (Brown 1985), but no focused studies have tested this hypothesis. The close association of *Placidula* and *Brugmansia* suggests a dependence on some compounds from these plants, with chemical protection derived from this relationship.

Adult Biology

The differences in the seasonal changes of population size of *P. euryanassa* between Ribeirão das Pedras and Morro do Japuí probably are due to climatic differences in these two places. In March, *P. euryanassa* is rather common in Ribeirão das Pedras (where the temperature is colder than in Morro do Japuí) and the population begins to increase, while in Morro do Japuí this increase happens only in May. The severity of the winter in Ribeirão das Pedras (June–July) could determine the low number of adults after June. It is possible that adults migrate to warmer places on the coastal plain or die due to low tem-

peratures (K. Brown pers. comm.). However, the population increases during this period in Morro do Japuí, where the winter has milder temperatures (never less than 8°C). Ribeirão das Pedras may be colonized each year in the early autumn (March–April), until the population decreases abruptly in late winter (July–August). In Morro do Japuí, the population appears to be maintained at low densities during the summer (November–March), increasing by reproduction and migration in late autumn (May–June). Although tropical butterflies may have constant populations with little variation throughout the year (Benson & Emmel 1972, Ehrlich & Gilbert 1973), *Placidula euryanassa* shows a considerable fluctuation in size throughout the year, a pattern also reported in other Ithomiinae (Vasconcellos-Neto 1980). This picture of fluctuation in size is more common in temperate species (Ehrlich 1984) and reinforces the idea that *Placidula* is a subtropical genus (Brown 1979).

Male-biased sex ratios in the field have been observed many times in butterflies, even when the sex ratio in the laboratory is 1:1 (Brussard & Ehrlich 1970, Brussard et al. 1974, Brown & Ehrlich 1980, Matsumoto 1984, 1985). Behavioral differences between males and females probably account for this “catchability difference” between sexes (Ehrlich 1984). In *Placidula euryanassa*, the same situation was observed. The difference in catchability can be related to the frequent visitation to sources of pyrrolizidine alkaloids by males (Brown 1985).

The age structure of *P. euryanassa* through time, from a predominance of new individuals in the beginning of each population peak to old individuals at the end of the peak, suggests that each population peak can be considered as an eclosion period (i.e., one generation of *P. euryanassa*).

Vagility data indicate that all capture sites in Morro do Japuí represent a single population of *P. euryanassa*; the population may be even larger than estimated (Fig. 4). Capture points were closely related to nectar sources, and dispersal between sites occurred whenever a new nectar source became available.

The time of residence indirectly reflects survivorship of the adults (Ehrlich 1961, Ehrlich & Gilbert 1973); *Placidula* shows a low survivorship compared with other Ithomiinae butterflies (Brown pers. comm., Freitas unpubl.). According to Brown and Ehrlich (1980), data obtained as time of residence are distributed as a truncated Poisson curve, as in the present study (Table 3). Thus it is not possible to test significance of difference of residence times calculated from these data against previously published residence times. Low permanence of females in a population can be explained by high dispersal, as happens with *Actinote pellenae pellenae* (Hübner) (Nymphalidae: Acraeinae) (Francini 1989). The survivorship curves of adult males and females are of type

II. Although type II curves are most common in K-strategists (Pianka 1970), other features suggest that *P. euryanassa* is an r-strategist. Among these are low survivorship of the adult, great number of eggs, easy colonization of secondary environments, rapid decrease of the populations ("catastrophic" mortality), short time of larval development and instability of the populations of this species. All these factors contrast with those of long-lived K-strategist butterflies such as *Heliconius* (Ehrlich & Gilbert 1973, Gilbert 1991) and many other Ithomiinae (Vasconcellos-Neto 1980, 1986, 1991).

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SCOLIOPTERYX LIBATRIX (NOCTUIDAE) AND TRIPHOSA HAESITATA (GEOMETRIDAE) IN CAVES IN MANITOBA, CANADA

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ABSTRACT. The troglaxene moths *Scoliopteryx libatrix* and *Triphosa haesitata* found in small caves in Manitoba, Canada, were studied over a two year period. Fewer individuals of the latter species were found (126:54), but both species overwintered in caves in which the temperature remained above freezing. *Triphosa haesitata* tended to seek sites further from the cave entrance and preferred slightly warmer air temperature and greater relative humidity than *S. libatrix*. These findings may be related to the fact that *T. haesitata* is near the northern limit of its range. Noteworthy was the finding that some specimens (about 10%) of both species remained in the caves throughout the year. These may represent a portion of the population that spends a second concurrent winter underground prior to leaving the caves the following spring. In the laboratory, at cave temperature (5°C), adult *S. libatrix* remained viable up to 14 months after capture.

Additional key words: ecology, humidity, temperature.

In Manitoba there are three areas where bedrock dissolution has produced such features as the famous "snake pit" sinkholes and the more recently discovered myriad of small caves. The caves are located in three areas: near Gypsumville, Hodgson, and Grand Rapids in the Interlake region of the Province (Fig. 1). Sweet et al. (1988), Voitovici and McRitchie (1989), McRitchie and Voitovici (1990), and McRitchie (1992) describe these caves in detail.

Two moth species were seen repeatedly in 16 of 26 caves investigated. A widespread Holarctic species, the herald moth, *Scoliopteryx libatrix* (L.), was observed in 14 caves and a second species, the tissue moth, *Triphosa haesitata affirmaria* Walker, was noted at 10 of the 26 caves investigated. Findings in the current study support those described earlier by Banta (1907) in America, and Roeder and Fenton (1973) in Canada, on *S. libatrix*. Kowalski (1965) also provided similar ethological and ecological data on *S. libatrix* and *Triphosa dubitata* L. in Poland. Peck (1988) and Peck and Christiansen (1990) refer to these species as troglaxene, meaning they use caves regularly to overwinter but are unable to complete their life cycle within the caves. This paper reports information gathered on these moths; no other insects were observed regularly in the Manitoba caves.

METHODS AND MATERIALS

Twenty-six caves were investigated for the presence of insect life. Sixteen caves were selected for further study as these repeatedly contained either or both species of moths. From April 1989 to October 1990 I visited these 16 caves at least twice and one site known as Window

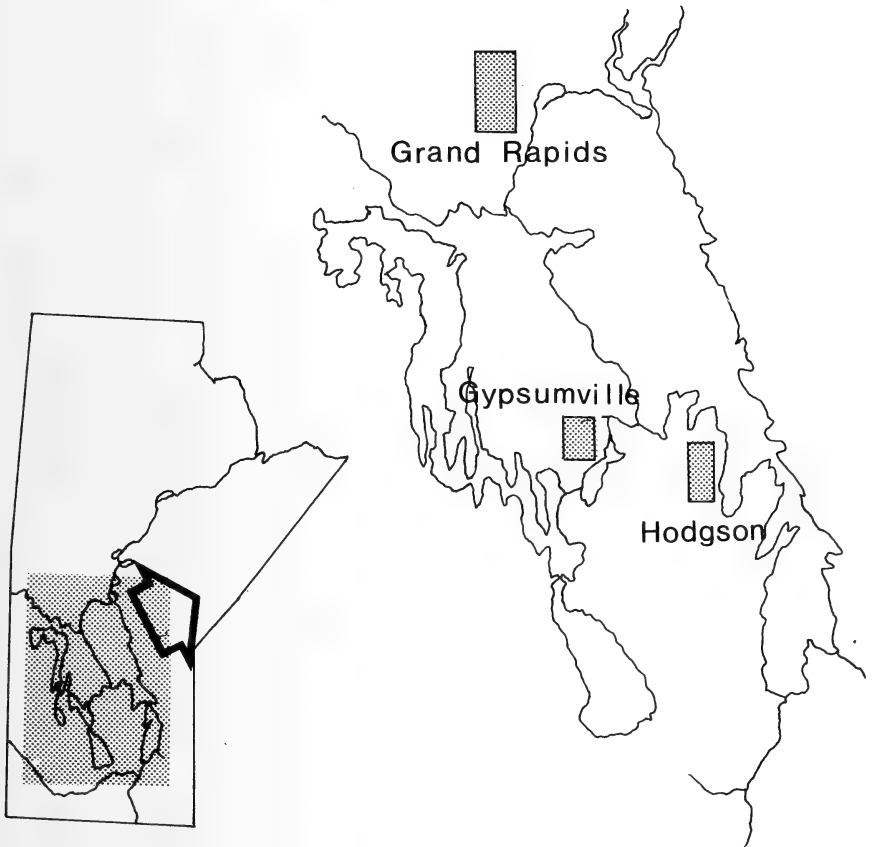


FIG. 1. The location of major cave regions in Manitoba, Canada.

Cave was visited four times. The presence and number of each species of moth was recorded. Voucher specimens were collected and deposited in the Manitoba Museum of Man and Nature. Air temperatures were measured in the caves routinely both years using hand held thermometers, while minimum/maximum thermometers were used in Firecamp and Window caves. Relative humidity measurements were taken using a portable psychrometer (Model 566-3 Bendix Psycron) in the 1990 field season. The presence of air currents was monitored by observing the smoke trail from an extinguished match. Live specimens of *S. libatrix* and *T. haesitata* were taken to the laboratory for further study.

RESULTS AND DISCUSSION

Moths were among the few insects observed in the caves and the only insects studied in detail. Other notable finds included members of

TABLE 1. Physical features of 16 selected caves.

Cave location and name	Length (m)	Depth (m)	Opening		<i>S. libatrix</i>	<i>T. haesitata</i>
			1	2		
Gypsumville						
Crystal Kingdom	21.0	3.8		*	*	
Long Crawl	125.5	3.0	*		*	*
Maze	76.5	1.2		*	*	
Chamber	55.0	1.4		*	†	*
Stormcloud	—	—	*		*	
Phantom Bear	39.5	5.5		*	*	*
Grand Rapids						
Squeaky	15.5	6.2	*		*	*
Knoll Chimney	19.0	14.0	*			*
Dale's	35.5	5.5	*		*	*
Bear	7.5	3.5	*		*	
Microwave #1	24.6	9.8	*		*	
Microwave #2	25.0	10.0	*		*	*
Firecamp	26.0	8.0	*		*	*
Ice	10.5	5.0	*		*	*
Hodson						
Window	67.6	7.9	*		*	*
Bat's Cave	165.3	12.5	*		*	

* The presence of a particular attribute or species.

† In 1991 the Speleological Society of Manitoba (McRitchie 1992) observed *S. libatrix* in Chamber cave but no additional data was recorded, and so this finding is of distributional interest only.

the Diptera: a new species of midge closely related to *Camptocladius stercorarius* (Degeer) (Chironomidae) currently thought to be a monotypic genus which breeds in dung; *Exechiopsis* sp. (Mycetophilidae) frequently found in cavities on the forest floor; and *Anopheles earlei* Vargas (Culicidae) known to overwinter in caves (Price et al. 1960).

Both species of moths were taken in each of the three areas of caves. Covell (1984) lists the food plants for *S. libatrix* as willow and poplar (Salicaceae), both of which were abundant at all cave sites. The food plants listed for *T. haesitata* are not in the area or are nearing their northern distributional limit. The documented host plants, including wild plum (Rosaceae), oak (Fagaceae), and barberry (Berberidaceae), were not found here, while buckthorn (Rhamnaceae) and hawthorn (Rosaceae) are rare. This may explain, in part, the greater total number of *S. libatrix* found in the caves.

Although individuals of the two moth species were not observed moving in or out of the caves, the numbers of both species increased in the autumn and declined in spring as recorded by both Banta (1907) and Kowalski (1965). Within the caves movement of individual moths was observed, although this was very local and limited to only a few cm over a season. Kowalski (1965) noted much greater movements within caves subject to rapid temperature shifts, but in caves with a



FIG. 2. Two specimens of *Scoliopteryx libatrix* on the ceiling of Window Cave.

temperature regime like that of the Manitoban caves movement was restricted to simply changing orientation or moving but a few cm, findings similar to mine.

While the majority of moths left the caves in spring, some remained in the caves throughout the summer. Nine *S. libatrix* and six *T. haesitata* were observed in the twelve caves investigated in the summer. I initially believed that these individuals would leave the caves, but by autumn they remained where they had been in the spring. Both Banta (1907) and Kowalski (1965) commented on finding dead, fungus covered moths in caves. Although approximately half a dozen dead, fungus covered moths were observed during the study, the individuals that remained in the caves throughout the summer appeared viable. These moths may represent a portion of the population that hibernates over two successive winters thereby providing these species with an alternate life history strategy that may be important in the harsh northern climate. Alternatively, they may simply have a higher activity threshold temperature and do not respond to the slight warming temperatures in spring. Nevertheless, specimens of both species taken into the laboratory in late summer and held at a temperature of 5°C with high humidity (90–100%) survived to the following spring, suggesting an ability to overwinter for two successive winters. Adult *T. haesitata* remained viable for 8–10 months while *S. libatrix* lived for slightly longer periods. No specimens of either species lived beyond 14 months in captivity. Hence, it is unlikely a second summer can be passed in the caves.

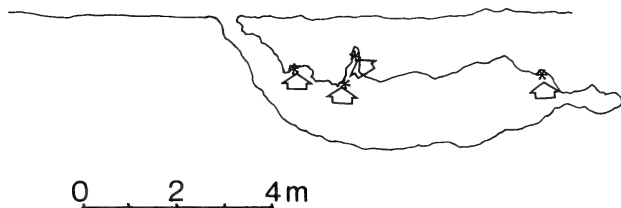


FIG. 3. A cave schematic showing sites where the two moth species frequently hibernate.

Specifications for the various caves investigated are provided in Table 1. Twelve of the caves have a single entrance but four had two or more entrances. In the latter category, slight air currents were encountered confirming connection with the surface although the other entrances could not always be found. Moths were not observed in such "open" sites but were found in side caverns or cul-de-sac passages. The distance from the entrance to the location of the individual moths varied between species. *Scoliopteryx libatrix* was found somewhat closer to the opening, i.e., 1–10 m (\bar{x} = 3.8 m), while *T. haesitata* usually was found further into the caves, i.e., from 2.5–12 m (\bar{x} = 5.2 m). Both species stayed within the proximity of the entrance.

Moths were observed in dry areas of the caves, often near the ceiling, and usually in groups numbering two to six individuals in close prox-

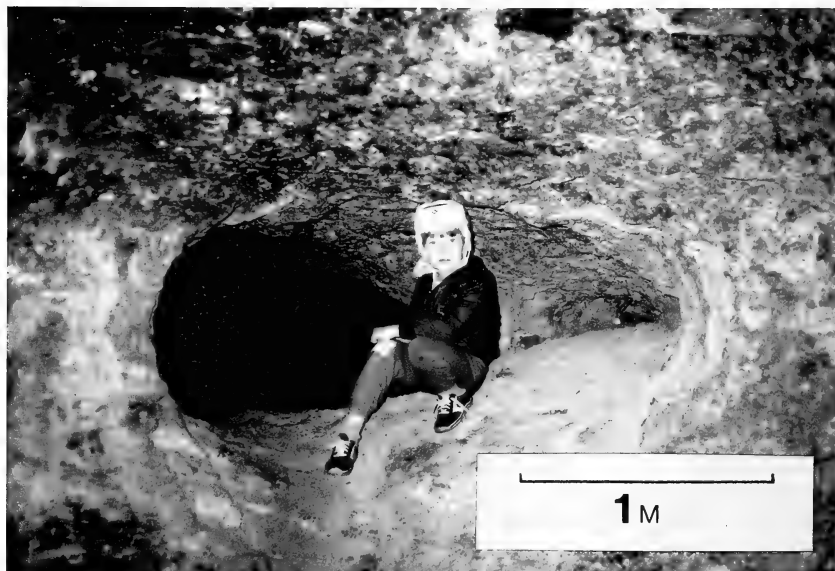


FIG. 4. General nature of cave interior showing cul-de-sac side passages and ceiling features including rocky ridges and algal growth.

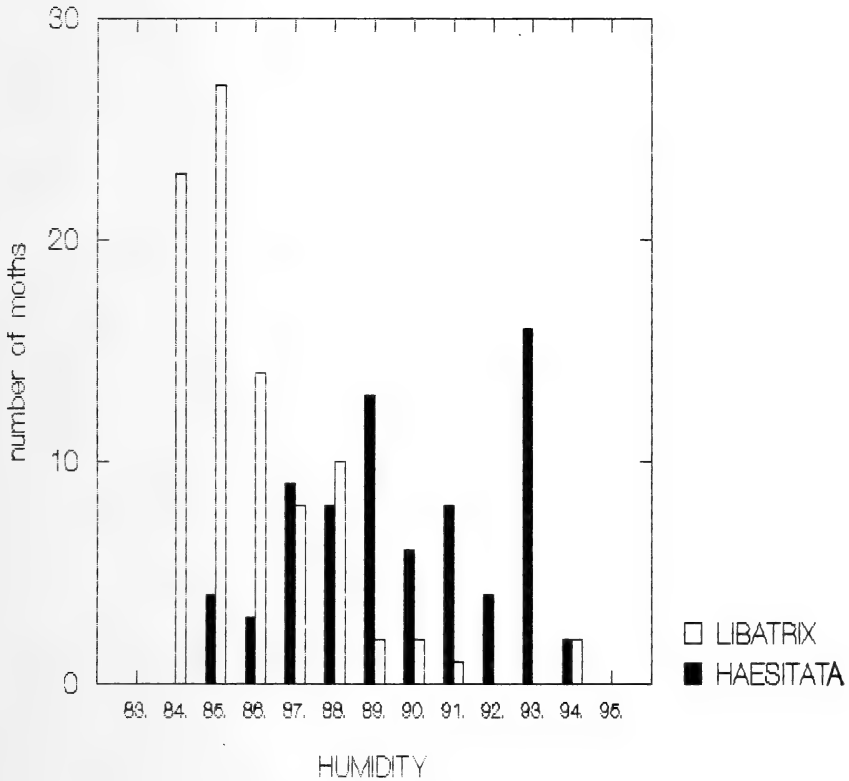


FIG. 5. The distribution of *Scoliopteryx libatrix* and *Triphosa haesitata* in relation to humidity.

imity (Fig. 2), a finding similar to that of Kowalski (1965). Sites most frequented were dry, hollowed out ceilings, tubes running vertically up from the ceiling, and areas just beyond rock lips on the ceiling (Figs. 3 and 4). Little air current was noted here despite being near the entrance of the caves. Low light levels and algal growth often were evident within a meter or two of these sites (Fig. 4). Whereas the relative humidity in the caves varied, only those caves with humidity in excess of 84% contained moths. Figure 5 shows the number of moths collected in relation to relative humidity. *Triphosa haesitata* favored sites with somewhat higher humidity, with the majority in the 87–93% range; most *S. libatrix* were taken in the 84–88% range. Like Kowalski's (1965) findings, water droplets frequently were observed on the moths' bodies and wings, but unlike his findings ice crystals were not seen on the moths because cave temperatures in which overwintering moths were observed remained above freezing.

Caves containing moths maintained a narrow above-freezing temperature regime throughout the year, with a mean of 5.4°C and a range of 3–9°C, while ambient temperature outside was \pm 40°C. Firecamp and Window caves had annual minimum/maximum temperature ranges of 5.5/7.5°C and 4.8/8.9°C respectively. The air temperature in caves increased slowly in spring, and between April and June warmed from 3°C to 6°C with a mean of 5°C. During the summer, twelve caves, including Crystal Kingdom, Long Crawl, Maze, Squeaky, Dale's, Bear, Microwave #1, Microwave #2, Firecamp, Ice, Window, and Bat's Cave were visited, and these remained between 6–9°C. The mean air temperature in areas occupied by moths during the eight month period from April to November during both years was 6.5°C for *S. libatrix* and 7.4°C for *T. haesitata*. In September to November the caves cooled from 9.0°C to 3.5°C with a mean of 6.2°C. My findings support those of Banta (1907) who noted that cave temperatures in spring when *S. libatrix* leave Mayfield's cave were cooler than when they return in the autumn.

ACKNOWLEDGMENTS

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REDISCOVERY OF *HYALOPHORA EURYALUS CEDROSENSIS*
(SATURNIIDAE), WITH DESCRIPTIONS OF THE
ADULT AND LARVAL STAGES

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ABSTRACT. We report the rediscovery of *Hyalophora euryalus cedrosensis* (Cockerell) from Isla de Cedros, a small island off the western coast of Baja California, Mexico. The adult and larval stages are described and compared with nominotypical *H. e. euryalus* (Boisduval). The known distribution of *H. euryalus* on the peninsula of Baja California, Mexico is reviewed.

Additional key words: Mexico, California, Baja California, Isla de Cedros, endemism.

Since its brief description in a footnote by T. D. A. Cockerell (Packard 1914:226), the taxonomic status of *Hyalophora euryalus cedrosensis* has been uncertain. It was described from a "suffusedly blackened" male collected on "Cedars Island," Mexico. Cockerell characterized this subspecies as follows:

"Male. Margins of upper side of wings broadly and suffusedly blackened, the submarginal markings almost entirely lost; ocellus of primaries smallish; discal mark on hind wings longer and more slender than in *kasloensis*; beneath the wings are very black, but the region basad of the bands is suffused with brownish vinaceous."

The type locality of this taxon is most certainly Isla de Cedros, situated off the west coast of Baja California, Mexico, about halfway down the peninsula (west of Guerrero Negro). The type specimen could not be found and no specimen labelled "Cedars Island" or "Isla de Cedros" could be located in any of the major U.S. museum collections (Ferguson 1972). Sweadner (1937) treated *H. euryalus cedrosensis* as a separate species (i.e., *Platysamia cedrosensis*) but commented that it was only a "list" name due to the lack of a type or other specimen from the presumed type locality. Hoffmann (1942) and Rindge (1966) treated *H. e. cedrosensis* as a subspecies. Bouvier (1936), Ferguson (1972), and Lemaire (1978) treated *cedrosensis* as a synonym of *H. euryalus eu-*

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Isla de Cedros

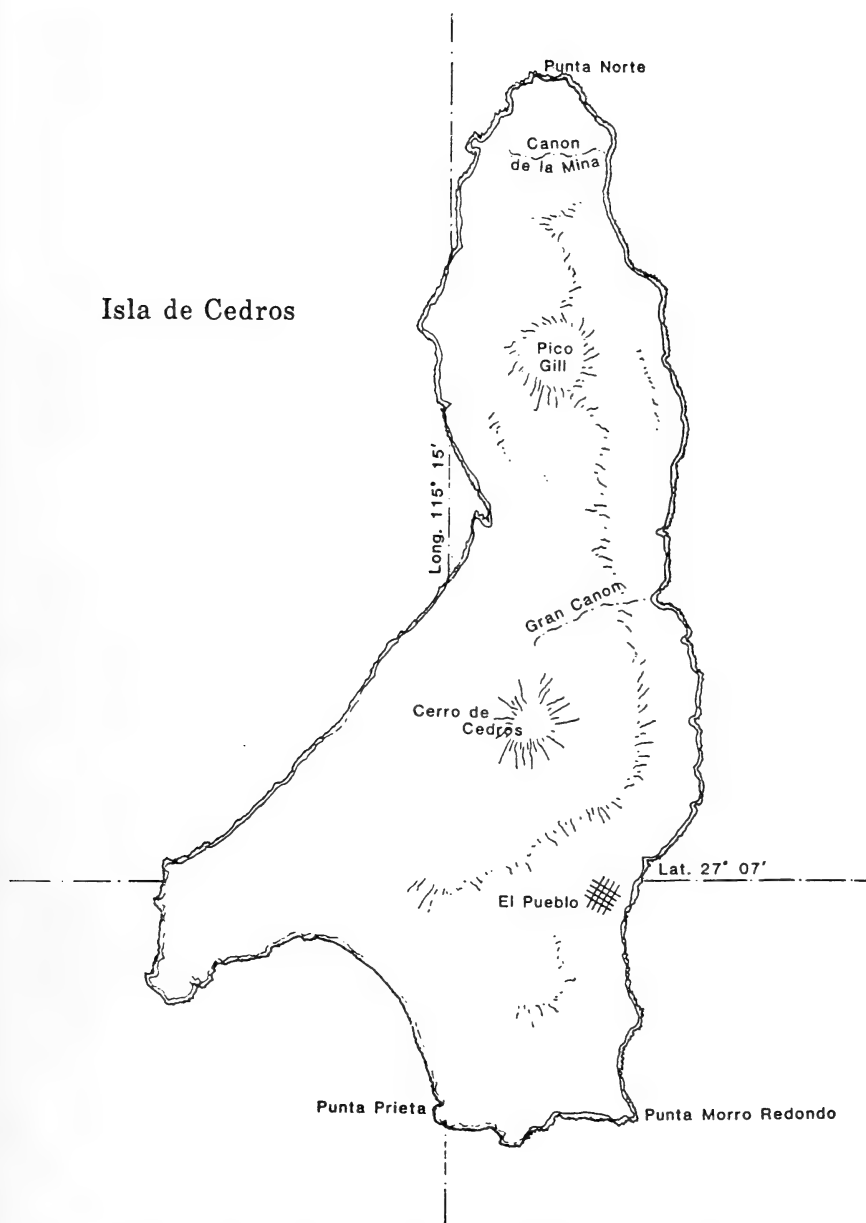


FIG. 1. Map of Isla de Cedros, Baja California Norte, Mexico.

ryalus primarily owing to the absence of a type specimen or any other material available from Isla de Cedros.

During a trip to Isla de Cedros in May 1986, one of us (REW) discovered cocoons of *H. euryalus* on shrubs at the mouth of the Gran Canyon on the east side of the island. On a later trip in January 1987, a female *H. euryalus* was attracted to a propane camp light at the mouth of Gran Canyon. Since then, a total of three males and two females have been collected at light at the mouth of Gran Canyon by R. Wells. Also, a series of adults has been reared from four larvae collected in the Gran Canyon area or from eggs obtained from field collected adults. Examination of these specimens and comparison with adults and larvae of *H. e. euryalus* from California and peninsular Baja California have allowed us to confirm the integrity of *H. e. cedrosensis* as a distinct subspecies of *H. euryalus*, and to provide a more thorough description of this insular subspecies.

TYPE LOCALITY

Isla de Cedros (Fig. 1) is a mountainous island of 348 square km located off the west coast of Baja California. It is 34 km long and 4–15 km wide. The north-south mountain spine contains a few prominent peaks, the highest of which is Cerro de Cedros at 1200 m. The largest intrusion into this mountain chain is the Gran Canyon located midway on the east side of the island. The island's geographic position results in inconsistent and infrequent moisture from northern winter storms and from southern tropical summer storms ("chubascos"). The island receives frequent moisture from dense fog year-round (Libby et al. 1968, Lewis & Ebeling 1971). The habitat at Gran Canyon, where *H. e. cedrosensis* has been collected, has a fairly impoverished flora that includes buckwheat (*Eriogonum fasciculatum* Nutt., Polygonaceae), lemonadeberry (*Rhus integrifolia* [Nutt.] Rothr., Anacardiaceae), laurel sumac (*Malosoma laurina* Nutt., Anacardiaceae), California juniper (*Juniperus californica* Carr., Cupressaceae), elephant tree, (*Pachycormus discolor* [Benth.] Cov., Anacardiaceae) and agave (*Agave shawii* var. *sebastiana* [Greene] Gentry, Agavaceae) (Wells pers. obs.).

Geologically, Isla de Cedros represents the northern extension of the extensive Sierra Vizcaino of the Baja mainland (Gentry 1950, Wiggins 1980). However, the island's flora and butterfly fauna have strong affinities with the Californian Biotic Province that occurs considerably further north (Moran 1972, Gould & Moran 1981, Brown & Donahue 1989, Brown & Faulkner 1989, Langston 1980). The island supports many plants typical of the Vizcaino-Magdalena Province of the adjacent mainland, including the elephant tree and agave (mescal). However, the number of Californian Province elements reaching their southern

limits on Isla de Cedros demonstrates that the primary relationship of the island's flora is to the north, with the Californian Province, a phytogeographic region that extends from the California border south to the vicinity of El Rosario, Baja California Norte. Remnants of this habitat also are found on some mainland Baja California mountain peaks south of El Rosario (Gould & Moran 1981, Brown & Faulkner 1989).

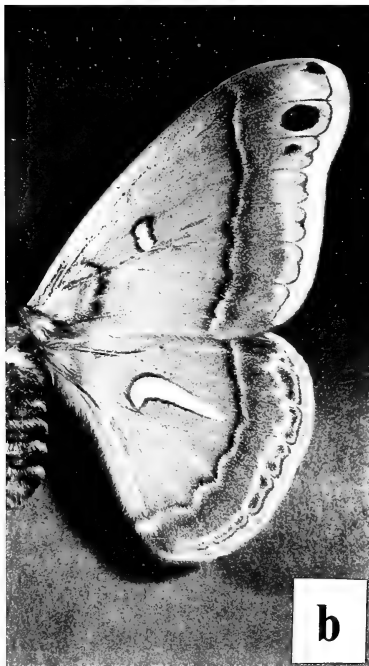
During two visits to the Gran Canyon by the junior author, the island was in the midst of a drought. Evergreen shrubs, such as *Rhus*, *Juniperus*, and a few others, comprised the only green vegetation. Flowers were virtually absent and only 14 species of butterflies were collected. The windward west side and north end of the island were greener because tall vegetation there precipitates water from the fog.

SYSTEMATICS

Hyalophora euryalus cedrosensis Cockerell

The description below is based on two males and two females collected as adults or cocoons on Isla de Cedros, and an additional eight males and ten females reared from eggs obtained from wild collected females, all by the junior author. Measurements are from the four collected adult specimens; descriptions of color pattern are based on wild collected and reared specimens because there was no observable color variation.

Male (Fig. 2a). Forewing length 48.6 mm and 59.0 mm, $n = 2$. *Antenna*: Brown, very fan-shaped. *Head*: Covered with dark lavender hair. *Thorax*: ground color dark lavender-brown hairs, white collar behind head, bordered with darker, longer lavender hairs posteriorly. Legs covered with lavender-brown to lavender hairs. Band of light tan hair at posterior edge of thorax. *Abdomen*: Base color dark lavender-brown, each segment ringed by a partial to full band of white hairs. *Dorsal wing surface*: Deep maroon-red; white antemedial and postmedial lines variably obscured by black scales, creating dark gray color in most specimens. Central portion of forewing postmedial line most heavily obscured, nearly obliterating postmedial line in most specimens. Black line basal to postmedial line wavy. Forewing discal spot creamy white, small; hindwing discal spot concolorous with FW spot, elongate, often extending distally to postmedial line. Dorsal hindwing discal spot in strong contrast with dark ground color. Usually a black submarginal spot in cell M_1-M_2 ; often less distinct submarginal spots in M_3-Cu_1 and Cu_1-Cu_2 , occasionally also in M_2-M_3 . Apical black spot relatively large and prominent in margin of dorsal FW. Apical eyespot in cell R_5-M_1 nearly uniform black, with a thin bluish line in basal section. Outer half of margin variable from light to dark brown, depending on degree of black scaling on wing surface. Veins connected by a sharply delineated black line immediately basal to margin. Spot $R_{3+4}-R_5$ with whitish S-shaped line between black apical spot and eyespot. Hindwing margin brown with blackish spots and dashes at posterior end of each cell. *Ventral wing surface*: Dark, almost mahogany brown. Costal region and area distal to postmedian line heavily sprinkled with white. Submarginal band essentially concolorous with ventral wing ground color. Margin medium brown, with blackish to dark brown dashes at posterior end of each cell. Eyespot in cell R_5-M_1 blackish with blue shadow in basal half.



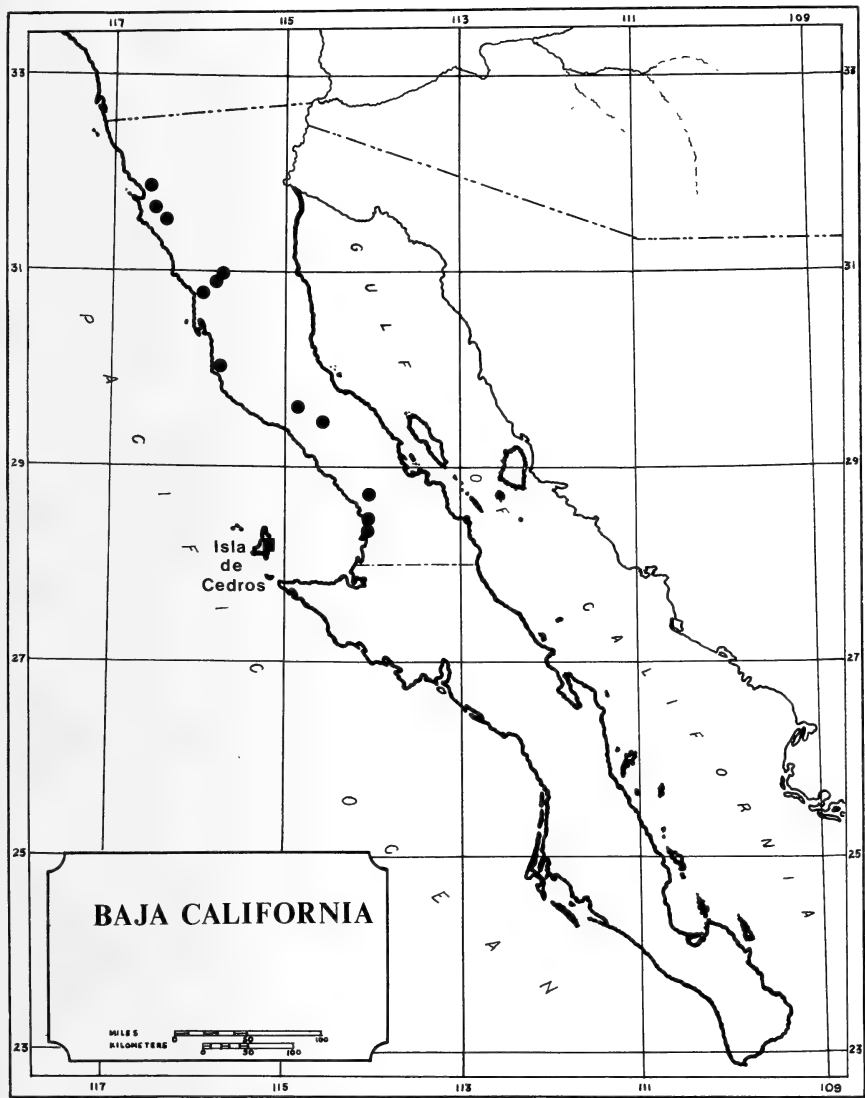


FIG. 3. Distribution of *H. euryalus* in Baja California, Mexico: closed squares = *H. e. cedrosensis*; closed circles = *H. e. euryalus*.

FIG. 2. Adult *Hyalophora euryalus*: a. *H. e. cedrosensis* male; b. *H. e. cedrosensis* female; c. *H. e. euryalus* male from mainland Baja California peninsula; d. *H. e. euryalus* female from mainland Baja California peninsula.

Female (Fig. 2b). Forewing length 60.9 mm, $n = 1$ (the other wild caught female too damaged to measure). Wing surface characters essentially the same as in male.

Topotypical pairs are deposited in the collections of the Universidad Autónoma de Ensenada, Ensenada, Baja California Norte, Mexico, and San Diego Natural History Museum, San Diego, California.

Distribution. The distribution of *Hyalophora euryalus euryalus* in Baja California is shown in Fig. 3. All wild caught specimens of *Hyalophora euryalus cedrosensis* are from Gran Canyon, Isla de Cedros, Baja California, Mexico.

Larvae. Description based on 20 larvae obtained from eggs deposited by two female specimens collected on 3 January 1987 and 6 January 1987, Gran Canyon, Isla de Cedros, about 40–60 meters from the water's edge. All larvae were reared by REW on California peppertree (*Schinus molle* Linnaeus, Anacardiaceae).

First instar. Emerged between 31 January 1987 and 8 February 1987. Length at emergence 4–5 mm; length prior to molt 10–11 mm, width 2.0–2.5 mm. Larval color predominantly black, some individuals (about 20%) with yellow-orange at the base of the thoracic tubercles. Some anterior spines tinted orange. Instar lasted 7–10 days.

Second instar. After molt, length 11–13 mm, width 2.0–2.5 mm. Head and all legs black. Ground color variable from nearly solid black (most) to dull yellow-green. Darkest larvae with orange spots at base of each dorsal tubercle; some orange spots enlarged, contiguous with adjoining spots, creating an orange-green longitudinal stripe on the back. Orange-green stripe widening to create yellow-green ground color in some individuals. Dull yellow-green larvae variable from dark to bright. Brightest larvae yellow-green with only the tubercles and legs black. Tubercles enlarged in 2nd and 3rd thoracic segment and 1st abdominal segment; tubercles slightly enlarged on 2nd abdominal segment. Tubercle singular and prominent on 8th abdominal segment. Spines and tubercles most prominent in this instar with greatest tubercle to larval body size ratio. Instar lasted 7 days.

Third instar. After molt, length 13–25 mm, width to 4 mm. Head black with inverted dull green "Y" in center. True legs black, prolegs dull green blotched with black. Tubercles and spines black. Thorax and abdomen dull green with dull yellow-orange patches. Some larvae with yellow-orange patches on lateral surfaces. Tubercles enlarged on 2nd and 3rd thoracic, and 1st and 8th abdominal segments. Spines prominent after molt, decreasing in prominence as larvae expand during growth. (Consistent for all instars.) Spiracles black. Instar lasted 9 days.

Fourth instar. After molt, length 24–53 mm, width 7–10 mm (11–12 mm at dorsal segments). Head 2.5–3.0 mm, dull green and black. Ground color dull green with no segmental markings; many individuals diffuse to dull black from mid-lateral to ventral surface (this is a 4th instar characteristic disappearing in the 5th instar). Tubercles enlarged on 2nd and 3rd thoracic and 1st abdominal segments; these have base color orange, ringed and spotted irregularly with black (some examples are totally black). Tubercles bulbous in the middle, spines reduced and more bristlelike, some light orange basally. Tubercles smaller on 2nd through 7th abdominal segments; orange with small black bristles; end spike of these most prominent. Tubercle on 8th abdominal segment singular, centrally located, orange and unmarked (except in a few specimens that are lightly spotted with black). Lateral tubercles black, usually with black spines. Some specimens with median row of tubercles dull green centrally, with black spines and black base. Two specimens with central green area white. Spiracles white. Instar lasted 9 days.

Fifth instar (Fig. 4a). After molt, length 53–90 mm, width 10–15 mm. Head and legs light green; prolegs light green with dark gray pads. Body color uniformly dull green transitioning to a darker green (dull black tone) ventrally, without the relatively sharp delineation between green and blackish of the fourth instar. No conspicuous black or orange markings. All lateral tubercles short, rounded, white, including those anterior to large dorsal tubercle on 8th abdominal segment. Row of tubercles nearest prolegs shorter, broader, and rounder; upper medial tubercle row longer, thinner, and more pointed. Dorsal tubercles on 2nd and 3rd thoracic and 1st abdominal segments enlarged (3.0–3.5 mm), light yellow, ringed by typical equatorial band in the middle. Dorsal tubercles on 2nd through 7th abdominal segments smaller, lighter yellow (occasionally flecked with

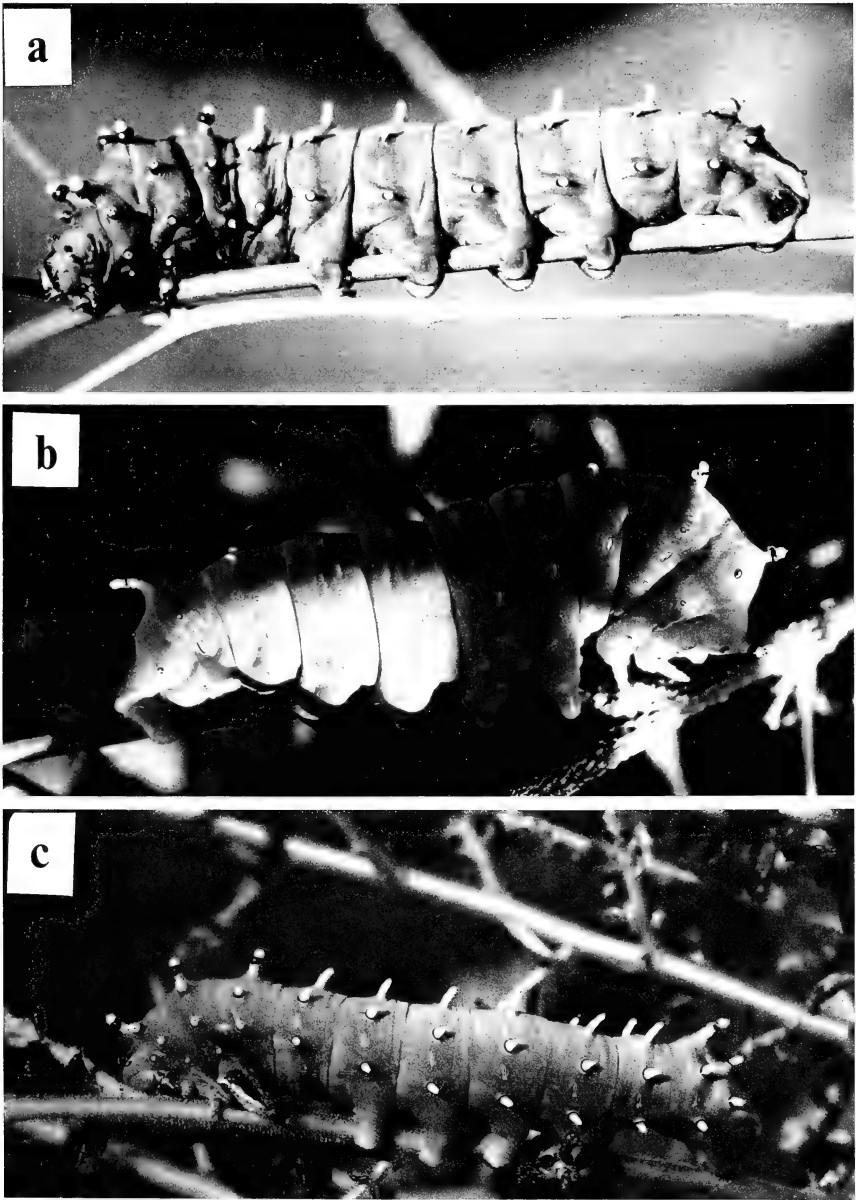


FIG. 4. Final instar larvae of *H. euryalus*: a. *H. e. cedrosensis* from Isla de Cedros, Baja California Norte, Mexico (photo by R. Wells); b. *H. e. euryalus* from El Socorro, Baja California Norte (mainland), Mexico (photo by M. J. Smith); c. *H. e. euryalus* from Orinda, San Mateo Co., California (photo by F. McLaren).

black), with no change in basal color. Tubercle on 8th abdominal segment singular, 3 mm long, lacking bulbous black ring, but flecked with black. All tubercles with minute black bristles on the tips; most tubercles black basally. Spiracles white.

DIAGNOSIS AND DISCUSSION

Hyalophora euryalus cedrosensis can be distinguished from *H. e. euryalus* by its darker color and the more prominent appearance of the hindwing discal spots (see Fig. 2). The deep maroon-red of the dorsal wing surface is darker than the variable pink-red (lavender) to red-brown of *H. e. euryalus*. The darkest specimens of the nominotypical subspecies tend toward dark brown rather than to maroon-red as in *H. e. cedrosensis*. The second most notable difference, and most diagnostic, is the sooty black suffusion of the postmedian line in *H. e. cedrosensis*, especially on the forewing. This is the character described by Cockerell (in Packard 1914), and it is consistent in all specimens examined. Sweadner (1937) incorrectly suggested that this black suffusion was caused by soot from the oil lamps that attracted the suspected (unlabelled) specimen of *H. e. cedrosensis* he studied. The dark ventral surface described by Cockerell is variable from black-brown to dark brown, but tends to be darker than in nominotypical *H. euryalus*. The outer third of the dorsal surface of *H. e. cedrosensis* is darker than the basal two-thirds owing to the black scaling, thus differing from the lighter pinkish-red to red-brown of the outer third of *H. e. euryalus* (see Collins 1984). The abdominal color of *H. e. cedrosensis* is a dark maroon-red compared to the brighter reddish lavender of *H. e. euryalus*. On the mainland of Baja California, *H. euryalus* is found from the California border, south to about 69 km north of Guerrero Negro (see Fig. 3). Mainland populations fall within the range of variation of California *H. e. euryalus*. Although the Baja California specimens tend to be redder (female specimens browner) than those of California, we consider them to be nominotypical *H. euryalus*.

In general, larvae of *H. e. cedrosensis* are darker or possess more black markings (or both) than larvae of *H. e. euryalus* in all instars (see Fig. 4). Only the first instar in the nominotypical subspecies is all black, whereas many individuals in the second instar of *H. e. cedrosensis* are totally black. In the middle instars, this black color is displaced by shades of yellow and dark green; however, the green of even the final instar always retains the dusky, charcoal pigment in *H. e. cedrosensis*. Larvae of *H. e. cedrosensis* never have the bright, almost pearly-green appearance of the mainland subspecies.

Larvae of *H. e. cedrosensis* feed on *Malosma laurina* and *Rhus integrifolia*, and on the Baja California endemic *Pachycormus discolor* (all Anacardiaceae); the latter is a new foodplant record for the species.

Rhus lenti Kell. (Anacardiaceae) also occurs on Isla de Cedros and hybridizes with *R. integrifolia* where the two species are sympatric (Young 1978). The preferred foodplant on Isla de Cedros appears to be *Malosma laurina* since the greatest percentage of cocoons were found on this species. The use of *Pachycormus discolor*, originally discovered on Cedros, has been confirmed for the mainland subspecies (Wells pers. obs., Tuskes pers. comm.). We observed no significant differences between the cocoons of the two subspecies.

The consistency of adult and larval differences between *H. euryalus* and *H. euryalus cedrosensis* indicate that *H. e. cedrosensis* is sufficiently distinct from *H. e. euryalus* to be considered a valid subspecies endemic to Isla de Cedros. The lack of variation in *H. e. cedrosensis* follows Mayr's (1976) founder principle wherein it is postulated that original colonists to the island would have contained less genetic variability than mainland populations. Evolution would occur more rapidly in the island population because of its genetic isolation (see Peigler 1989:115). *Hyalophora euryalus cedrosensis* was isolated on Isla de Cedros along with other remnants of the Californian Biotic Province; this pattern is illustrated by the butterfly fauna (Brown & Faulkner 1989). Based on Moore (1969) and Minch et al. (1976), the formation of the modern basins along the continental borderland west of the peninsula of Baja California dates from mid-Pliocene times and was followed by a marine regression from the close of the Pliocene, the Pleistocene, and Holocene times. Thus *H. e. cedrosensis* may have been isolated from the mainland since the early Pliocene. Owing to the considerable distance, gene flow between the mainland and insular populations is probably low.

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BIOLOGY OF THE RARE SKIPPER, *PROBLEMA BULENTA* (HESPERIIDAE), IN SOUTHERN NEW JERSEY

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ABSTRACT. The rare skipper, *Problema bulenta* (Boisduval & Leconte), was first recognized as occurring in southern New Jersey in 1989, although the first specimen was collected in 1983. Through the summer of 1992, it has been found in five counties along the Delaware bayshore and the Atlantic coast, with Burlington Co. the northern limit. We collected two larvae in the field on *Spartina cynosuroides* (L.) Roth (Poaceae), and reared one to maturity on the same host. Adults occur in tidal marshes containing *S. cynosuroides*, but have been observed only in the vicinity of nectar plants, not in patches of the larval host. Adults may become highly concentrated on nectar plants at some sites; we have counted as many as 121 individuals on flowers in ten minutes at one locality. It is not yet possible to say whether the New Jersey populations are secure.

Additional key words: tidal marsh, *Spartina cynosuroides*, distribution, larva, host-plant.

The rare skipper, *Problema bulenta* (Boisduval & Leconte 1833), was originally described from a John Abbot drawing based on a specimen from Georgia (Harris 1972, Miller & Brown 1981). It was not collected again until the 1920's near Wilmington, North Carolina (Jones 1926, Klots 1951). Since then it has been found further north in Virginia (Covell & Straley 1973) and Maryland (Opler & Krizek 1984). It seldom has been found in large numbers and the hostplant has not been reported. It is currently a candidate for listing as threatened or endangered under the U.S. Endangered Species Act.

In early July 1989, each of the authors collected a single female near brackish tidal marshes, one in Cape May Co. and the other in Atlantic Co., New Jersey. Subsequently, Schweitzer found a specimen among a group of papered Lepidoptera that he had collected in Cape May Co., 3-8 July 1983. The present study was undertaken to determine the distribution and biology of this little-known species in New Jersey.

METHODS

In 1990, 1991, and 1992, we conducted searches by foot and automobile in tidal wetlands along the southern New Jersey shore. Sites were selected based on similarity to the localities of our original captures, the presence of suspected hostplants, and presence of known nectar plants. United States Geologic Survey 7.5 min quadrangle maps

were used to select candidate areas. Several sites that contained very little or none of the suspected host, *Spartina cynosuroides* (L.) Roth (Poaceae), were searched: the Brigantine Division of Forsythe National Wildlife Refuge, the marshes west of Port Norris, and the Heislerville Wildlife Management Area. The first two of these were searched repeatedly.

Searches and counts were visual, sometimes aided by binoculars. At least one voucher specimen was taken for every site, and subsequently one or more individuals were netted for positive identification each time a site was visited. At no time did we collect large series; the most examples collected on any day was 9, when 121 were seen in ten minutes.

Because nearly all temperate Hesperinae feed on Poaceae or Cyperaceae, and because *Problema byssus* (Edw.) feeds on large grasses (Opler & Krizek 1984, Scott 1986), we attempted to induce oviposition by captive females and rear the resulting larvae on several species of grasses and *Scirpus* from the brackish marshes. These studies were carried out indoors at ambient temperature (18–27°C) and without humidity control. Females collected in the wild were caged with cut sections of plants and a supply of sugar or honey water. Newly hatched larvae were placed in small plastic boxes with leaves of *S. cynosuroides*, *Phragmites australis* (Cav.) Trin. (Poaceae), and two unidentified weedy grasses. The larvae were provided with fresh leaves every 24 to 48 hours. On 1 and 2 August 1990, small groups of eggs and larvae were placed in sleeves tied over single shoots of *P. australis* (1 sleeve) and *S. cynosuroides* (2 sleeves) in a brackish tidal marsh.

Searches for larvae in the field were made by walking slowly through or around patches of the suspected hosts and checking any plants that showed chewing damage on leaves. Searches were conducted in early September 1990 and in late May and early June 1991. The most thorough searches were conducted at two sites, one which had an abundance of adults in 1990 and the other where fewer adults had been seen. Areas with suspected hosts where no adults had been observed were checked as well.

RESULTS AND DISCUSSION

Distribution and Habitat

In the summers of 1990–92, *P. bulenta* was found in marshes of two streams emptying into Delaware Bay, at several widespread locations along its shore in the extensive marshes with numerous small creeks, and in two major river basins on the Atlantic coast. It is now known from Salem, Cumberland, Cape May, Atlantic, and Burlington counties.

Opler's (1992) reference to this species' occurrence in New Jersey is based on these records. It has not yet been found on the Cape May peninsula, where suitable habitats are not extensive. Cromartie searched brackish marshes along the Atlantic coast in Ocean Co. and Monmouth Co. in 1991 and 1992, but found no *P. bulenta*. In 1992, the species was reported from marshes along the Delaware Bay in Delaware (Smith & Cohen 1992).

With the exception of one specimen, all *P. bulenta* taken or observed in New Jersey to date have been in tidal marshes or on flowers in old fields within a few hundred m of such habitats. These habitats tend to be mosaics of a variety of grasses and graminoids including *Spartina cynosuroides*, *Phragmites australis*, *Scirpus* spp. (Cyperaceae), *Acorus calamus* L. (Araceae), and *Typha* sp. (Typhaceae). Some sites are essentially saltmarshes dominated by *Spartina alterniflora* Loisel., *S. patens* (Ait.) Muhl., and *Distichlis spicata* (L.) Greene (Poaceae), with less salt tolerant plants like *S. cynosuroides*, confined to upland edges and streambanks. Upstream on the larger rivers these habitats grade into freshwater tidal marshes characterized by *Zizania aquatica* L. (Poaceae), *Peltandra virginica* (L.) Kunth (Araceae), and *Pontederia cordata* L. (Pontederiaceae).

The most conspicuous forbs in these habitats are *Hibiscus palustris* L. (Malvaceae), *Kosteletzkya virginica* (L.) K.B.Presl (Malvaceae) and *Asclepias incarnata* L. (Asclepiadaceae). In early summer, there are often no nectar bearing flowers available in the marshes, but by the end of the flight season, *H. palustris* is widely available in the less saline habitats.

On 8 July 1992, a single male was collected in a garden in Port Republic, Atlantic Co., New Jersey, about 0.6 km from the nearest tidal marsh. A probable second individual was seen there on 4 August, nectaring on ornamental *Liatris spicata* (L.) Willd. (Asteraceae), an early-flowering cultivar.

Oviposition by Captive Females and Rearing Attempts

Females oviposited readily in captivity on a variety of grasses, but laid most eggs on *Spartina cynosuroides* and *Phragmites australis*. When confined with a weedy *Panicum* sp. (Poaceae) alone, they oviposited on its short, wide leaves. Females also oviposited on filter paper and the sides of containers. Generally, fewer than twenty eggs per female were obtained.

The eggs are flattened, hemispheric, about 0.6 mm in diameter, and pale cream color when newly laid, quickly becoming more yellowish. Eggs hatched in approximately eight days when kept indoors; we es-

time hatching would take a day or two longer in the field where nighttime temperatures would be lower. The newly hatched larvae are greenish white with black heads, and are about 3–4 mm long. Two or three larvae constructed small retreats near the tips of *Phragmites* leaves by folding over the edges and tying them with about seven short silk threads. The tips beyond the retreats showed chewing damage. None of the larvae survived to second instar; they appeared to have difficulty feeding on the rather tough dry leaves that were available in mid-July. The attempt to rear larvae by sleeving them was unsuccessful.

The Larva and Hostplant

Four hours' search among stands of *S. cynosuroides* on 1 and 3 September 1990 failed to uncover any larvae or retreats of the kind made by the captive larvae. An hour or two of searching near Delaware Bay, in June 1991, on *S. cynosuroides* only, produced no larvae or signs of feeding. On 29 May 1991, Cromartie found a 2.4 cm long larva in a tubular retreat on a leaf of *S. cynosuroides* growing on the edge of a road in Atlantic Co. The larva was brought into the lab and fed fresh leaves, on which it constructed a new shelter. After five days it left the plant and moved to the upper corner of the cage where it constructed a thin layer of silk and was observed to forcefully expel a small, dry fecal pellet. The larva returned to food the next day but was listless and did not appear to feed. It died on 9 June.

On 6 June, after a total of twelve hours searching over seven days, Cromartie found a second larva in a tube on *S. cynosuroides* growing next to a small bulkhead on a paved road in southern Burlington Co. This larva constructed new retreats and fed on leaves of *S. cynosuroides* in the lab until 21 or 22 June, when it sealed itself into its tube. It pupated in the last larval tube, which it probably first reinforced with additional silk. Part of the tube was cut away to prevent injury from shrinking plant tissue, but the pupa was left in place. On 6 July, a male *P. bulenta* that lacked orange scales on both forewings eclosed.

The larva (Fig. 1) is pale green with an indistinct blue-green dorsal stripe. The transverse folds of the body have darker green marks. There are paired dark spots, one pair per segment on the dorsal side and smaller pellucid dots over the entire body. The only vestiture is short white hairs on the dorsal terminal plate. The "neck" is paler and more yellow. The head is light brown with paler vertical markings and a dark brown stripe from the vertex down both sides. Our larvae are similar to, but not quite identical with, the one figured in Boisduval and Leconte (1833, plate 67).

Based on the pattern of adult occurrence as well as the two larvae found, we believe that *Spartina cynosuroides* is the primary, if not

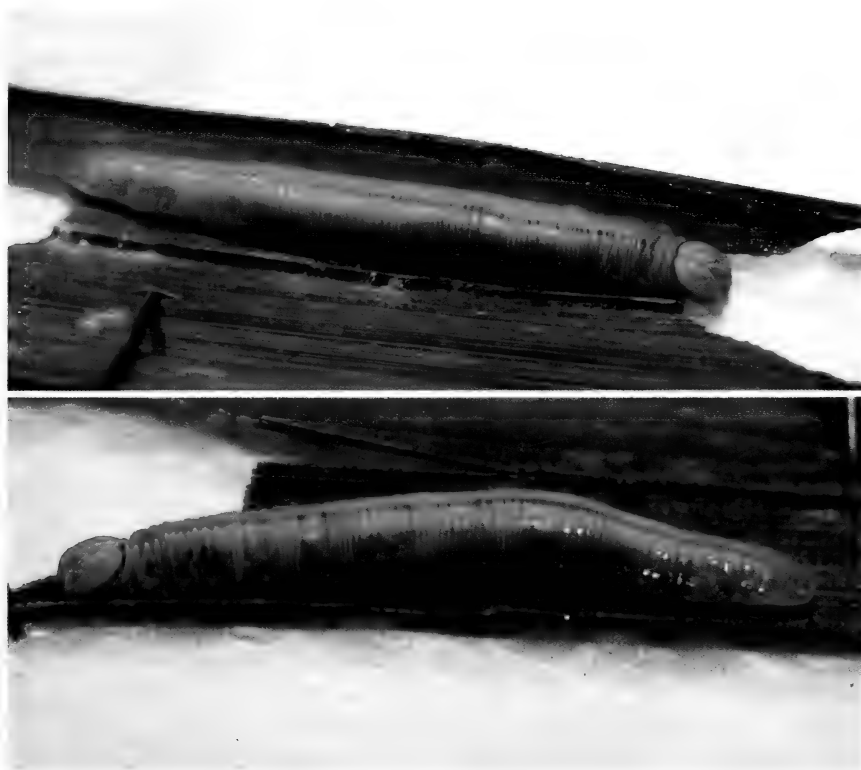


FIG. 1. Larva of *Problema bulenta*, collected 6 June 1991, Burlington Co., New Jersey, and reared on *Spartina cynosuroides*. Photographed 11 June 1991. Length, approx. 30 mm. Emerged 6 July 1991.

only, host for *P. bulenta*. Various authors (Opler & Krizek 1984) have suggested *Zizaniopsis miliacea* (Michx.) Doell and Aschers. (Poaceae) as the host, but the northernmost occurrence of *Z. miliacea* is in Maryland. Moreover, it does not occur near the known Maryland site of *P. bulenta* (Schweitzer pers. obs.; Maryland Natural Heritage Program). *Spartina cynosuroides* occurs throughout the known range of *P. bulenta* and beyond, from Texas to southern Massachusetts (Fernald 1950, Duncan & Duncan 1987). There are stands of this grass at the Wilmington, North Carolina sites. As far as we can determine, the skipper is always found in tidal marshes where this grass is characteristic. It is a robust, rhizomatous perennial, usually 2–3 m tall. Shoots begin growing in April in southern New Jersey, and die back in late October or November, although some dry culms remain standing until the next season.

Spartina pectinata Link, which is similar to *S. cynosuroides*, occurs

on the upland side of brackish marshes and along roadsides and ditches. It, too, might be used but is probably too scarce in southern New Jersey to be an important hostplant. Moreover, it does not occur south of New Jersey (Fernald 1950, Duncan & Duncan 1987). We also consider *Phragmites australis* and the tall form of *S. alterniflora* found in brackish marshes to be potential foodplants. It is possible, however, that this skipper will prove to be monophagous on *S. cynosuroides*. Our failure to find the skipper at the Brigantine National Wildlife Refuge, at Port Norris and at Heislerville, where nectar plants, *P. australis* and *S. alterniflora* are abundant, but *S. cynosuroides* is extremely scarce or absent, supports this tentative conclusion.

Adult Seasonal Occurrence and Behavior

Problema bulenta appears to be single brooded in southern New Jersey. From 1983 to 1990, and including 1992, our earliest date for adults is 4 July and the latest is 9 August. In 1991, however, which was probably the most advanced Lepidoptera season in this century in New Jersey, adults were observed 24 June, in numbers by 26 June (J. Dowdell pers. comm.) and were declining by 15 July. Oddly, we have collected only one really fresh adult (a male, 26 July 1992) in four years; perhaps they wear quickly due to their powerful flight.

Adults are most abundant at flowers between 1000 h and 1400 h. The latest we have collected one is 1745 h. Unlike some other large skippers, adults are quite active on warm overcast days. Males and females seem to be nearly equally abundant; twenty-two males and thirty females were counted at one site on 16 July 1991. The highest single daily count was 121 in a span of ten minutes at one site on 21 July 1990. As many as fifteen adults may occur on a single inflorescence of *A. incarnata*. They are never territorial or pugnacious around flowers. The adults are so passive when visiting flowers that they can be collected without a net; the best specimens are obtained by collecting directly into a killing jar.

More than ninety-five percent of the adults observed or collected have been nectaring on flowers in or at the edges of brackish tidal marshes or in nearby fields, along rights of way, or other similar habitats. The most highly favored nectar plants are swamp milkweed (*Asclepias incarnata*) and buttonbush (*Cephalanthus occidentalis* L., Rubiaceae), but we have seen them regularly on *Hibiscus palustris*, *Kosteletzkya virginica*, *Asclepias syriaca* L. and *Apocynum cannabinum* L. (Apocynaceae), and occasionally on *Daucus carota* L. (Apiaceae), *Pontederia cordata*, *Cirsium* sp. (Asteraceae), white *Eupatorium* sp. (Asteraceae), *Centaurea* sp. (Asteraceae), *Vicia* sp. (Fabaceae) *Saponaria officinalis* L. (Caryophyllaceae), *Ipomoea* sp. (Convolvulaceae), *Trifolium pra-*

tense L. (Fabaceae), and the ornamentals *Liatris spicata* (one sight record) and *Hibiscus syriacus* L.

There are several nectar sources frequented by other skippers in the same habitat that apparently are not utilized by *P. bulenta*. These include *Teucrium canadense* L. (Lamiaceae), a native *Lythrum* sp. (Lythraceae), and *Vernonia noveboracensis* (L.) Michaux. (Asteraceae).

Apart from those feeding on flowers, we have encountered only a few individual adult *P. bulenta* resting on *Phragmites australis* near nectar sources and one female flying near *Spartina cynosuroides*. *Problema bulenta* flies very fast and usually 1–2 m above the tall grasses, making it very difficult to follow. Schweitzer was able to observe an undisturbed individual leave a nectar site in an old field. The skipper spiralled almost straight up to about 25 m, then turned and flew over a patch of forest in the direction of a tidal marsh. One other nectaring area is largely surrounded by forest, so this behavior is probably common.

Despite hours of walking through stands of *S. cynosuroides* we have never encountered adult rare skippers there, and despite the density of adults on flowers at some sites we had little success finding larvae on *S. cynosuroides* growing near those areas. We believe that this skipper must range very widely over the brackish marsh. It may in fact be rather scarce, with adults from large expanses of marshland becoming concentrated on the few available patches of nectar plants.

Our two larvae were found on plants along roadsides, although the searches were conducted both there and in stands well away from roads, and both were on plants that were not flooded at daily high tides. The preferred oviposition site may be plants on the relatively inaccessible upland edges where the marshes generally give way to dense hardwood or white cedar swamp forests. Flooding would be less severe there than in the open areas closer to the tidal creeks and rivers.

We are not yet sure of the precise habitat requirements for this species. In particular, it is unclear why we have not found it in numbers in the Great Egg Harbor River basin, which has large stands of *S. cynosuroides*, as well as normal populations of other marsh skippers. If adults tend to congregate at a few favorable nectar sites, it may be that we simply haven't found those particular sites, although our searches have included good patches of both swamp milkweed (*A. incarnata*) and buttonbush (*C. occidentalis*).

Status of the Rare Skipper in New Jersey

Given the attention that southern New Jersey has received from lepidopterists (Shapiro 1966), it would be surprising if they missed a conspicuous species like *P. bulenta* had it been present at its current

abundance before the late 1980's. Opler (1992) suggests it might have recently expanded its range into New Jersey, possibly in response to the series of record warm years in the late 1980's and early 90's. We believe that the species has been present and merely overlooked. Phenology and habitat may have contributed to this. Collectors venturing out to search for skippers such as *Panoquina panoquin* (Scudder) and *Poanes aaroni aaroni* (Skinner) are unlikely to be in the best habitats for *P. bulenta* at the right time of year. Mosquitos, tabanids, heat, and mud might discourage collecting trips in July, when no other generally desired species could be expected.

Collectors might also fail to recognize *P. bulenta* when seen. The Delaware skipper, *Atrytone logan* (Edw.), was observed at about half the sites where we found *P. bulenta*. While some tidal marsh populations of *A. logan* are bivoltine, flying before and after *P. bulenta*, others are univoltine and fly in July, as do all known inland populations in New Jersey. It is easy to confuse the male of *P. bulenta* with the female of *A. logan* in the field if only the underside is visible. They usually can be distinguished close up by the slightly different color of the underside and the longer, more pointed forewing of *P. bulenta*. It is possible that older papered material may include *P. bulenta* misidentified as *A. logan*.

Whether or not this species has recently expanded its range northward (Opler 1992), it is now probably widespread enough to be fairly secure from human threats to its persistence. However, adults sometimes are concentrated at the few available nectar sources, which presents the possibility of market-driven overcollecting. At several sites, careless net swings and trampling could easily destroy scarce nectar plants. We feel it is best to withhold precise locality data until the status of *P. bulenta* is better understood.

On the other hand, we would strongly caution against accepting sight records for new localities. Photographs may sometimes suffice for identification, but all new records should be verified by specimens because of the possibility of confusion with *A. logan*. Certainly current populations are large enough that collection of a small series poses no threat.

Voucher Specimens

The larva and the reared male have been deposited in the Yale University Peabody Museum of Natural History, and several wild collected males and females have been sent to Yale and to the Cornell University Entomology Collection. The remainder of our southern New Jersey specimens (a total of about fifty from four counties for 1989–92, counting the donated specimens and the remains of females kept for oviposition) are in the insect collection at Stockton State College and in the personal collection of Schweitzer.

ACKNOWLEDGMENTS

We thank Christian Adams for providing a set of color slides and the living female *P. bulenta* that so far constitute the only records for Salem County. Cromartie received Stockton State College Research and Professional Development funds for this work.

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MALFUNCTION OF ECDYSIS AND FEMALE BIASED
MORTALITY IN URBAN *BRASSOLIS SOPHORAE*
(NYMPHALIDAE: BRASSOLINAE)

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ABSTRACT. Adult mortality of *Brassolis sophorae* (L.) (Nymphalidae: Brassolinae) was studied on the State University campus in Campinas, São Paulo, Brazil, emphasizing mortality during ecdysis (pupa to imago). Four buildings were examined during the breeding season of *B. sophorae* in 1987 and 1989. The number of resting or dead adults were recorded and their weight and wing length were measured. The imagos from pupae attached to buildings suffered a high mortality and/or malfunction of ecdysis (nearly 20% of the individuals). High mortality was related either to direct human intervention, such as damage and removal of pupae and adults or to the use of smooth surfaces on the buildings by larvae for pupation. Smooth surfaces can cause difficulties in tarsal adherence of recently emerged adults. Females were significantly more subject to injury than males because (1) they usually rest on lower sites more susceptible to disturbance, and (2) they are heavier than males causing more difficulties in adhering to smooth surfaces during wing expansion.

Additional key words: urban ecology, urban insects, sexual dimorphism, butterfly mortality.

Adult *Brassolis sophorae* (L.) (Nymphalidae: Brassolinae) use human structures as resting sites and thus frequently are disturbed by man. On the campus of Universidade Estadual de Campinas (Campinas State University—UNICAMP) we observed many teneral adults of *B. sophorae* bearing nonfunctional or damaged wings. Malfunction of ecdysis is rare in natural populations of butterflies (Neck 1979). This contrasting situation led us to quantify the fates of emerging adults as well as the exploitation by this insect of building structures as resting sites. The adult stage usually has not been included in previous studies on the mortality of Lepidoptera in urban areas (Itô & Miyashita 1968, Sternburg et al. 1981, Ruszczyk 1986, Bastian & Hart 1990).

Brassolis sophorae is a crepuscular butterfly with a vestigial, non-functional proboscis. The gregarious larvae feed on palms (Arecaceae), both native (*Syagrus* spp., *Euterpe* spp., *Copernicia* spp.) and exotic (*Cocos* spp., *Washingtonia* spp., *Roystonea* spp., *Phoenix* spp.), and may become pests (Cleare 1915, Copeland 1921, Costa Lima 1936), even in highly developed sections of Brazilian cities (Ruszczyk unpubl. data). The larvae usually pupate in garages, retracted skirting-boards,

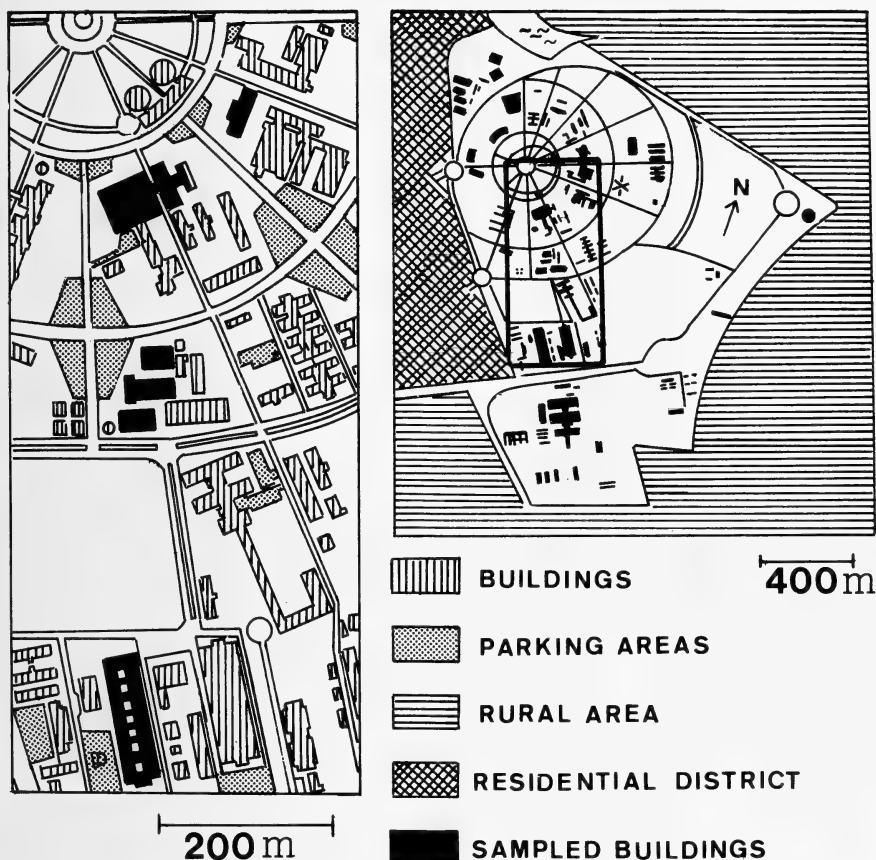


FIG. 1. UNICAMP campus (right map). Shaded buildings (left map) were daily censused for resting *Brassolis sophorae* during November–December 1987 and 1989. Shaded buildings from top to bottom, Physics Institute, Chemistry Institute, Food Technology Institute and Administration, respectively.

and mail boxes where a high pupal survival occurs because of partial protection against parasitoids (Ruszczyk unpubl. data). The life history of *B. sophorae* was described by Cleare and Squire (1934).

MATERIALS AND METHODS

Study Area

Four buildings on the UNICAMP university campus with palm trees [predominantly *Syagrus romanzoffiana* (Cham.) Glassman] planted near the walls were censused for resting and dead butterflies (Fig. 1, left). The campus (Fig. 1, right) is twenty-five years old and was landscaped intensively with both native and exotic trees. Large open lawns occupy

TABLE 1. Adult fate, resting site, and height of adult *Brassolis sophorae* recorded in four buildings at the Campinas State University. The frequencies of males (Ma) and females (Fe) in different situations were compared using Chi-square.

	1987		1989		Total	
	Ma	Fe	Ma	Fe	1987	1989
Adult fate						
Nonfunctional wings	23	40	2	24	63	26
Squashed (man)	3	23	—	12	26	12
Spider predation	5	4	1	1	9	2
Bird predation	—	2	—	12	2	12
Unknown mortality	3	7	1	3	10	4
Total	34	76***	4	52	110	56
Resting site						
Ceiling	69***	14	31**	21	83	52
Wall	32	50**	19	20	82	39
Column	27	13	9	19	40	28
Window sill	7	15**	2	6	22	8
Girder	6	6	10	5	12	15
Instrument box	9	6	2	4	15	6
Pipe	6	6	2	2	12	4
Window grating	3	1	—	3	4	3
Others	10	28	3	18	38	21
Total	169	139	78	98	308	176
Height						
Above 2 m	121***	61	59**	63	182	122
Between 0.3–2 m	45	63*	18	26	108**	44
Below 0.3 m	5	41***	9	30**	46	39
Total	171	165	86	119	336	205

* , ** , *** = $P < 0.05$, 0.01 and 0.001 , respectively.

most of the area. The buildings are surrounded by groups of common garden plants such as *Strelitzia reginae* Banks (Musaceae), *Acalypha wilkesiana* Muell. Arg (Euphorbiaceae), and *Rhododendron simsii* Planch (Ericaceae).

Data Collection

The buildings were surveyed daily for 2–3 h during breeding season (November–December) in 1987 and 1989. All adults found resting on the external walls and other structures were recorded. Notes were made on their sex, resting height, type of the resting site, presence of damaged wings (vestiges of beak marks) on the pavement, squashed individuals, and individuals with unexpanded or crumpled wings. In 1989, all individuals were collected and weighed, and the forewing length was measured. Chi-square tests were used to compare the frequencies of males and females in different heights, resting sites, and fates.

RESULTS AND DISCUSSION

A total of 127 adults died by squashing or malfunction of ecdysis (Table 1). These mortality factors affected females more than males, to varying degrees on different buildings. Females were preyed upon preferentially by a flock of guira cuckoo (*Guira guira* Gmelin, Cuculidae) that foraged daily in the palm trees of internal and external gardens. Predation was confirmed by direct observations of aerial attacks and collection of beak-marked wings. This visually oriented predator may select females due to their slower flight and larger body. Webs of *Nephilengys cruentata* Simon (Araneidae), an orb-weaver spider common in urban areas, were observed to have caught 11 individuals. It is common to find one or two *B. sophorae* in the same web. *Nephila clavipes* L. (Levi), another orb-weaver found infrequently on buildings, regularly catches butterflies in non-urban sites, but the predation is not species-specific (Vasconcellos-Neto & Lewinsohn 1984).

Brassolis sophorae is dimorphic; females are approximately twice as heavy as males (Fig. 2). Because the adult butterfly does not eat or drink, its maximum weight occurs at the time of emergence. The time interval from emergence to the first flight is greater than 24 h, exposing the insects to disturbance. The newly emerged imago is able to walk to the adjacent substrate to complete wing expansion. This behavior is highly adaptative in non-urban sites where the larvae usually pupate under debris, tree bark, or crevices and fissures in tree trunks.

In urban settings, however, many imagos are unable to hang onto smooth surfaces and fall. Such falls to the pavement often cause internal traumas and result in loss of internal fluids as evidenced by a film left on the pavement. Damaged butterflies usually crawled towards walls or man-made structures, continuing the process of wing expansion. Many individuals were squashed during this process. Being heavier than males, the females were more susceptible to falls from smooth surfaces.

The sexes differed in relation to resting site preference (Table 1). Males were found more frequently hanging onto the ceiling of protected walkways where they were partially protected from human interference, whereas females were found principally on walls and window sills. Males escaped more readily from humans and were less conspicuous owing to their smaller size.

In the two sampling periods, more than fifty percent of imagos observed were resting greater than 2 m above the surface, with a significant predominance of males at this height (Table 1). On the other hand, females were observed predominately below 2 m. This vertical stratification probably increased the risk of females being disturbed or

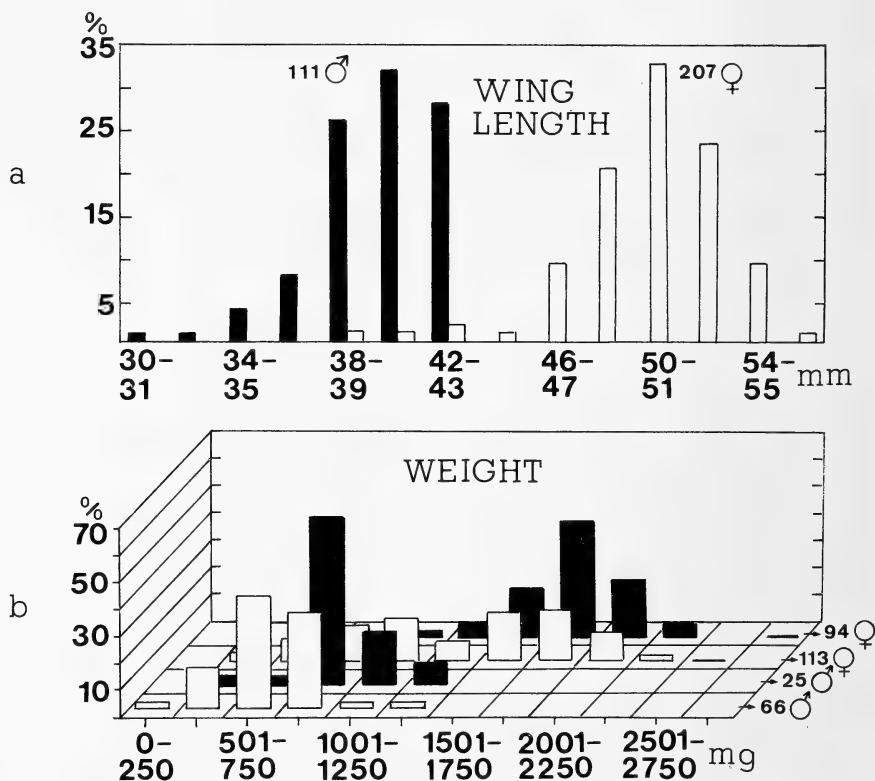


FIG. 2. Class distribution of adult male (shaded bars) and female (clear bars) wing-lengths (a). Class distribution of weight of newly emerged (shaded bars) and resting (clear bars) male and female of *Brassolis sophorae* collected at the UNICAMP campus.

squashed. The high frequency of human induced mortality factors and the female biased mortality suggest an adverse effect on the population. This high rate of mortality is in contrast to the rare malfunction of ecdysis observed in the wild. For example, Harcourt (1966) found a negligible number of dead adults of *Pieris rapae* L. (Pieridae) due to imperfect ecdysis.

It has been demonstrated that adult *B. sophorae* are selective in resting sites, in particular height. There were no significant differences in the data obtained in the two years sampled (last two columns of Table 1). The only exception was the number of individuals found resting at the height between 0.3 and 2.0 m. This suggests an incipient pattern of human architectural exploitation. Rather than the result of evolutionary change in response to specific urban selective pressures, this pattern may represent adaptation to the natural environment, such as the habit of resting in shaded places under similar materials used in

buildings. The details of human architecture may be physically similar to the shaded natural shelters.

In the butterfly's own world (in the sense of Uexkull 1909), a building may be perceived as a multifaced rock or tree trunk. The capacity of exploiting human structures as resting sites is an adaptive character of *B. sophorae* to the urban habitat where shaded and low temperature sites are not abundant, especially in the central areas of cities.

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A SUPERIOR TRAP FOR MIGRATING BUTTERFLIES

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ABSTRACT. Flight traps for studying butterfly migrations should be economical, efficient, and easy to construct, erect, service, and maintain. A 3-m-wide, semi-portable trap with these features was constructed of lumber, electrical conduit, braided nylon rope, and nylon-twine netting. Intercepted butterflies are guided into removable hardware cloth cages seated in metal trays at either end of the trap. These traps, which cost about \$50 each for materials and can be moved intact by two persons, caught the targeted migrants more efficiently than previous traps, including much taller and costlier immovable traps. They should foster and facilitate studies of migrating butterflies.

Additional key words: migration, *Phoebis sennae*, *Agraulis vanillae*, Florida.

Most migrating butterflies fly within a few meters of the ground and go over, rather than around, obstacles they encounter. This behavior makes migrants particularly susceptible to capture by flight traps, and such traps have been used for 17 years to study butterfly migrations in Florida and Georgia (Walker 1978, 1985a, 1991, Walker & Riordan 1981, Lenczewski 1992, Hatcher 1990). The earliest traps were made of mosquito netting and were fragile, squat, and inefficient (Walker 1978). These were superseded by permanent traps, made of hardware cloth on a steel and timber frame, that intercepted migrants flying as high as 3.3 m and were substantially more efficient (Walker 1985b). Need for inexpensive, portable traps prompted Walker and Lenczewski (1989) to develop traps of mosquito netting suspended from taut nylon ropes attached to end frames of electrical conduit. These traps had to be anchored and kept trimmed with guy ropes staked in four directions. Lenczewski (1992) used such traps to monitor migration along a 430-km north-south transect, and Whitesell successfully promoted their use by Georgia high school science students to trap migrants for marking and release (Hatcher 1990). The chief shortcomings of these traps were the large amount of sewing required to make them, difficulties in erecting, trimming, and maintaining them, their modest trapping efficiency, and the short outdoor life of the fabric. These problems, and the need for many more traps to service expanding studies of butterfly migration in Georgia schools, prompted us to design, construct, and test new traps. This article describes the trap that best combined low cost, ease of construction, efficiency, and durability and the 3 years of

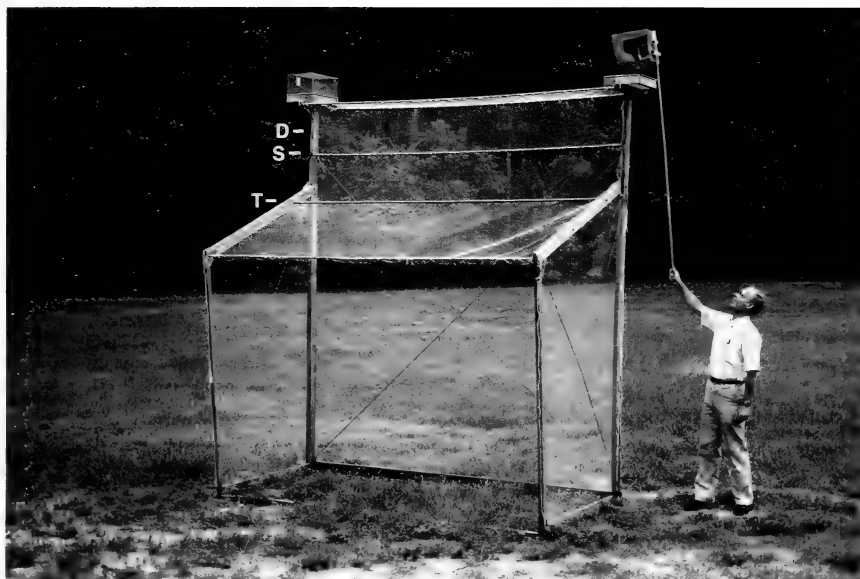


FIG. 1. Semi-portable trap, showing method of removing holding cage. Throat of trap begins at T and narrows to slot (S) through which migrants pass into triangular duct (D).

tests that led us to it. It is designated the semi-portable or s-p trap to distinguish it from the portable trap (Walker & Lenczewski 1989) and the permanent trap (Walker 1985b) developed previously.

THE SEMI-PORTABLE TRAP

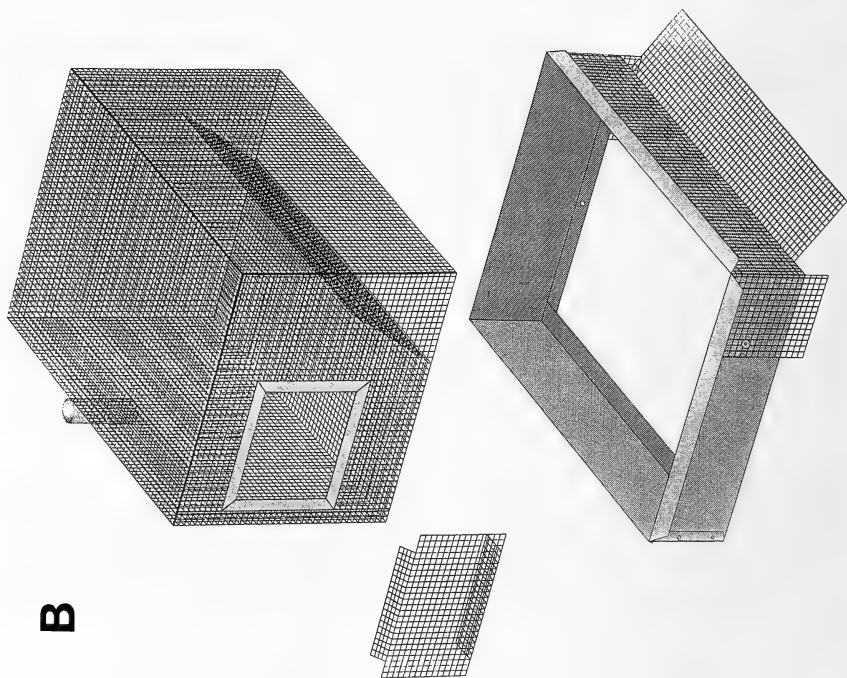
The s-p trap (Fig. 1) has a rigid frame of wood and $\frac{1}{2}$ " thin-walled electrical conduit (=EMT) internally braced with rope (Fig. 2A). Except for its bottom and a 3×2 m (w \times h) opening, the trap is covered with 13-mm-mesh, nylon-twine netting. Migrants that enter the trap encounter a wall of netting and, as they attempt to fly over it, flutter into a narrowing throat, through a slot, and into a duct that leads to hardware cloth cages held by metal trays at either end of the trap. The traps are set perpendicular to the direction of migration. If net movement in the migratory direction is to be quantified, half the traps are pointed upstream and the other half downstream. A stake at each inside corner keeps traps from blowing over. An Appendix gives details of construction.

TESTS OF TRAPS

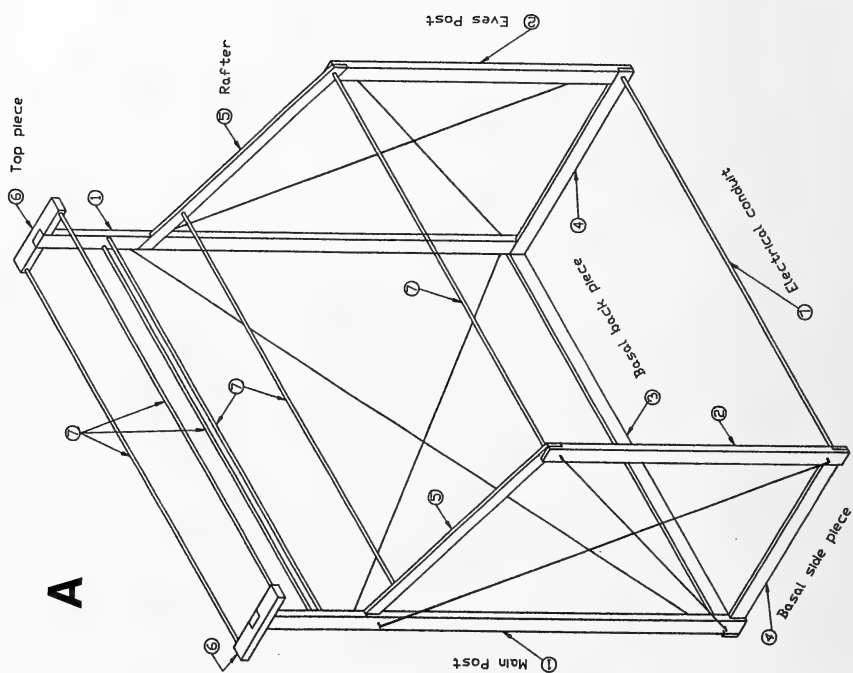
Materials and Methods

All tests were at the site of the two extant permanent traps (models #3 and #5; Walker 1985b). Trios of test traps were positioned to the

B



A



east and west of the permanent traps on the same ENE-WSW line as the permanent traps. Traps in a trio were about 1 m apart and faced WNW in fall and ESE in spring. Traps were serviced daily by removing and recording trapped butterflies, unless otherwise noted. To control for position effects, the traps in a trio were rotated periodically in their positions along the ENE-WSW line.

Fall 1988. Two frame designs and three fabrics were tested 9 September to 4 November by means of a trio of traps to the east of the permanent traps. The trio consisted of a *shrimp net* trap (s-p frame covered with 10-mm-square-mesh netting made of knotted 0.28 mm nylon monofilament), a *19-mm-mesh twine* trap (s-p frame covered with 19-mm-square-mesh netting made of #147 multifilament nylon twine), and a *no-throat* trap (s-p frame with the transition between rafters and slot eliminated, making the trap about 23 cm shorter but leaving the opening the same; covered with 19-mm-mesh twine netting until 6 October; on 6 October the fabric was changed to 13-mm-square-mesh netting made of double-knotted 0.28 mm nylon monofilament). Traps were rotated on 6 October.

Spring 1989. Three fabrics were tested 27 March to 29 May by means of two trios of traps. Each trio consisted of s-p frames covered with three fabrics: *shrimp net* (see above), *13-mm-mesh monofilament netting* (see above), and *13-mm-mesh twine netting* (13-mm-square mesh made of double-knotted #104 multifilament nylon twine). Traps were rotated on 22 April.

Fall 1989. Two fabrics and two catching systems were tested 12 September to 15 October by means of two trios of traps. Each trio consisted of a *standard s-p* trap (catching cage on both ends; covered with 13-mm-mesh twine netting), a *13-mm-mesh monofilament* trap (s-p frame covered with 13-mm-mesh monofilament netting), and a *one-cage* trap (like the standard trap except no opening in the netting and no catching device on the west end). Traps were rotated on 23 September and 4 October.

Fall 1990. Two catching systems and two trap heights were tested 29 August to 11 November by means of two trios of traps. Each trio consisted of a *standard s-p* trap (3.35 m main posts), a *one-cage* trap (see above), and a *12-foot* trap (same as standard s-p trap except all posts and the trap opening 0.3 m taller). Traps were run 29 August to

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FIG. 2. Construction details of semi-portable trap. A. Frame of 2 × 4 and 1 × 4 lumber and ½" EMT, braced at back and ends with diagonals of braided nylon rope. B. Holding cage (more details in Walker & Lenczewski 1989) and tray.

TABLE 1. Numbers of butterflies trapped during tests of semi-portable traps, fall 1989 and 1990. In 1989, catches of s-p traps were not significantly different for any species (ANOVA); in 1990, they were for *P. sennae* and marginally so for *A. vanillae*. S-p catches followed by same letter, in a column, are not different (least significant difference; $P = 0.05$).

Type of trap	Fall 1989			Fall 1990		
	<i>P.s.</i>	<i>A.v.</i>	<i>U.p.</i>	<i>P.s.</i>	<i>A.v.</i>	<i>U.p.</i>
Semi-portable traps (2 ea., 3-m)						
Standard	355	453	117	454a	678a	31
13-mm monofilament	293	451	122	—	—	—
12-foot	—	—	—	387ab	599ab	22
One-cage	286	425	82	329b	483b	20
Permanent traps (1 ea., 6-m)						
Model #3	372	245	196	327	357	63
Model #5	351	321	276	282	320	59
Relative efficiencies						
Std. s-p/avg. perm.	0.98	1.60	0.50	1.49	2.00	0.51

11 November and serviced every one or two days ($n = 39$). After service 13 and 26, traps were rotated.

Trapping efficiency. During 20 periods totaling 18.5 h, on 6 days between 27 September and 13 October 1989, migrants were watched as they encountered the trios of test traps. Migrants that were on a track leading to or over one of the traps were classed as "candidates," and candidates were scored as to their behavior relative to the trap: over, rise-and-over, in-and-over, through-slot-into-duct, etc.

Results

Fall 1988. Only the shrimp net trap (10-mm-mesh) caught migrants at a rate similar to the permanent traps. Per meter of trap, it caught 94, 115, 34, and 77% as many *Phoebis sennae* (L.) (Pieridae), *Agraulis vanillae* (L.) (Nymphalidae), *Precis coenia* (Hübner) (Nymphalidae) and *Urbanus proteus* (L.) (Hesperiidae) as the average of the permanent traps. The 19-mm-mesh netting allowed many migrating butterflies to pass through easily. The no-throat trap, even when covered with 13-mm-mesh fabric, caught fewer of the larger migrants than did the similar throated trap with 19-mm-mesh. For *P. sennae*, the totals were 82 and 111; for *A. vanillae*, 257 and 381.

Spring 1989. Per meter of trap, the shrimp net, monofilament, and twine traps caught 50, 13, and 20% as many *P. coenia* as the average of the permanent traps, which was 27.3/m. As usual, other spring migrants were scarce (≤ 5.2 /m).

Fall 1989 and 1990. Table 1 shows that the standard s-p trap performed better than any of its three variations, but only in 1990 were

differences significant or nearly so (ANOVA, *P. sennae*, $P = 0.04$; *A. vanillae*, $P = 0.11$). Least significant difference tests for catches of these two species in 1990 indicated that the standard trap was better than the one-cage trap in both cases ($P \leq 0.05$).

Trapping efficiency. S-p traps were more efficient at catching the larger migrants than were the permanent traps that separated the trios of test traps (Table 1). Per meter of trap, combining the data for fall 1989 and 1990, standard s-p traps caught 1.21, 1.82, and 0.50 times as many *P. sennae*, *A. vanillae*, and *U. proteus* as the average of the permanent traps. Direct observation of butterflies encountering the fall 1989 trios of test traps gave counts of 86 of 308 candidate *P. sennae* entering the ducts and 55 of 137 *A. vanillae*. Assuming that those in ducts make their ways into holding cages (which they generally do), the trapping efficiency and 95% confidence limits (based on binomial distribution) for *P. sennae* are $28 \pm 5\%$; for *A. vanillae*, $40 \pm 8\%$.

DISCUSSION

Few nonmigratory butterflies were trapped. Trapped butterflies were generally in good condition when removed from the holding cages, even when the traps were serviced at two-day intervals.

Of the four fabrics tested on the s-p frame, shrimp net (10-mm-mesh monofilament) was best for catching the smaller migrants. However, it caught *P. coenia* only 34 and 50% as efficiently as the permanent traps and *U. proteus* only 77% as efficiently. For the larger migrants, which were the ones we most wanted to catch, the 13-mm-mesh nylon-twine netting worked well. Traps with this fabric caught *P. sennae* and *A. vanillae* 121 and 182% as efficiently as the permanent traps. Traps with 13-mm-mesh monofilament and 13-mm-mesh nylon-twine netting did not differ significantly in their catches of *P. sennae* or *A. vanillae* (Table 1). An important advantage of 13-mm-mesh netting over the 10-mm-mesh netting required to catch the smaller migrants is its low wind resistance.

The importance of a throat—i.e., a gradual transition from the roof of a trap to the slot that accesses the duct—was first demonstrated in tests of permanent traps (Walker 1985b). The fall 1988 tests suggest that a throat is also important in s-p traps.

Having a tray and holding cage at each end of the trap adds to its cost and the time required to service it. However, in our tests of fall 1989 and 1990, traps with only one tray and cage caught 24 and 20% fewer *P. sennae* and *A. vanillae* than the standard s-p trap.

During direct observations of trapping efficiency, 44% of candidate *P. sennae* and 9% of candidate *A. vanillae* flew over the traps without going in. Consequently, increasing the height of the trap seemed a

promising means of increasing its efficiency. However, adding 0.3 m to the trap at the bottom, thereby increasing the height of its opening from 2.0 to 2.3 m, decreased numbers of target migrant caught by >10%. Perhaps more butterflies entered the trap but the roof and throat were no longer as effective at funnelling them into the slot.

When data from fall 1989 and 1990 are combined, the standard s-p traps caught 1.21 times as many *P. sennae* and 1.82 times as many *A. vanillae* as the average of the two permanent traps. These relative efficiencies, based on more than 2000 captured butterflies of each species, point the way to another means of estimating absolute efficiencies of the s-p trap. Walker (1985b) reported that 15.4 h observation of the Model #3 permanent trap in October 1984 yielded 96 and 52 candidates and estimated efficiencies of 49–70% and 22–50% for *P. sennae* and *A. vanillae* respectively. When the data in Table 1 are used to calculate the efficiency of the standard s-p trap relative only to the #3 trap, the numbers are 1.16 for *P. sennae* and 1.88 for *A. vanillae*. When these numbers are applied to the estimates of Model #3 efficiencies, inferred efficiencies for s-p traps are 57–81% for *P. sennae* and 41–94% for *A. vanillae*. Estimates of efficiencies for s-p traps based on direct observation were 23–33% for *P. sennae* and 32–48% for *A. vanillae* (see above). The two methods of estimating s-p efficiencies yield overlapping ranges for *A. vanillae* but not for *P. sennae*. Because sample sizes for estimating absolute efficiencies by direct observation were small, those estimates for either the #3 or the s-p traps (or both) are more likely to be non-representative than the estimates of the relative efficiencies of the two.

The ratio of *P. sennae* to *A. vanillae* in the permanent traps is significantly higher than that ratio in the standard s-p traps (2×2 contingency table; chi square, $P < 0.001$). It seems likely that the lower roof and throat of the s-p trap are more effective for the low-flying *A. vanillae*, while the high opening of the permanent trap intercepts more of the higher flying *P. sennae* (Walker 1985a, Fig. 1).

The fabric of our standard s-p trap proved appropriate to our needs, but other materials and meshes might have yielded larger catches. Indeed our data indicate as much for species other than *P. sennae* and *A. vanillae*. For studies lasting more than one year, a material more durable than nylon twine would be desirable. A candidate material is UV-resistant polypropylene netting, used for excluding birds from crops, which is reputed to last 5 yr outdoors. Tests of one such material (Ornex SM, Tenax Corporation, Jessup, Maryland) demonstrated that it was as effective as 13-mm-mesh nylon twine netting.

Compared to previously developed traps, the semi-portable trap com-

bines economy, efficiency, and ruggedness to a noteworthy degree. Materials cost less per meter of trap than for the portable and permanent traps. Making the trap and erecting it is easier and less time consuming than for the other two trap types. For our two target species, the s-p trap is the most efficient of the three. Routine maintenance and service is easier than for the portable trap and about the same as for the permanent traps. The chief way that the s-p trap does not equal or exceed both of the other two is in durability of fabric. In Florida weather, the polyester netting used on the portable traps lasted only a few months, but the hardware cloth of the permanent traps has lasted for more than 9 years. The nylon-twine netting of s-p traps fails in about 1 year—it is good for a fall and the following spring but will not last through the next fall. To sum up, the s-p trap has a combination of features that recommend its use in studies where butterflies migrating in the boundary layer are to be counted, marked and released, or collected for behavioral or physiological studies.

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APPENDIX: HOW TO BUILD TRAPS

Measurements are mostly in inches and feet, because the materials used were made and sold by those units ($1'' = 2.54$ cm; 1 ft = 0.305 m).

Frame. For each end, prepare a main post, eaves post, top piece, rafter, and basal side piece (132, 81, and 20" of treated pine 2×4 , and 65 and 58" of treated 1×4). Dado posts and top pieces as shown in Fig. 2A. The bottom of the dado for the rafter is at $100 \frac{3}{4}''$ on the back of the main post; its angle is 67.5° . Drill a $\frac{3}{4}''$ diam hole $\frac{3}{4}''$ deep to receive each of seven 10-ft lengths of $\frac{1}{2}''$ EMT (Fig. 2A). The center of the upper hole on the rafter is 1" from the upper edge and $15 \frac{3}{4}''$ from the upper end of the rafter. The lower hole on the rafter is 2 m above the bottom of the eaves post (making the trap mouth 2 m high). The EMT holes that define the slot of the trap are 18" from the top of the main post with centers $\frac{5}{8}''$ from either edge. Secure top piece to the main post with a $\frac{3}{8} \times 4''$ carriage bolt, and the rafter and basal side piece to the posts with four $\frac{5}{16} \times 2''$ stove bolts. On each end of the frame install four $\frac{1}{4} \times 2''$ eye bolts, eyes out, to secure the rope braces (see Fig. 2A). Install a $\frac{5}{16} \times 2''$ eye bolt with $\frac{3}{4}''$ diam hole, eye in, near each end of the basal side pieces, to receive stakes. With a helper, successively put in place the seven pieces of EMT and fasten each end in its $\frac{3}{4}''$ hole with a 6d galvanized common nail inserted in a $\frac{1}{8}''$ hole drilled through the wood and EMT. Nail the basal back piece ($121 \frac{1}{2}''$ of 1×4) in place.

Netting and braces. Install the main net (3 m \times 6 m) by stapling one end to the basal back piece and threading the other end through the slit, around the upper 2 pieces of EMT, back through the slit, under the EMT that defines the throat, and to the eaves. [We first used Stock No. 132, #104 multifilament nylon gill netting, $\frac{1}{2}''$ square, 102 mesh and 7 feet deep, purchased from Memphis Net & Twine Co., Memphis, Tennessee. We subsequently avoided having to staple and silicon-caulk two lengths together for the main net by special ordering double-depth (192 mesh, 14 feet) netting of the same type.] Starting at the basal back piece and keeping the net stretched, staple both edges of the netting to main posts, top pieces, main posts, and rafters. Staple the net to itself around the eaves EMT; then use silicon caulk to glue it to the EMT. Screw four $\frac{1}{4} \times 1''$ eyes into the main posts and install the rear braces of $\frac{3}{16}''$ braided nylon rope (Fig. 2A). Stretch and staple pieces of netting onto the ends and install the four ropes that brace the ends.

Trays and cages. Make each tray from a $4 \frac{3}{4} \times 56 \frac{3}{4}''$ piece of 20 ga galvanized metal twice bent longitudinally in a sheet metal break: 90° inward at 1" and maximally outward at 4" (Fig. 2B). At $11 \frac{1}{2}''$, 28, and $39 \frac{1}{2}''$ cut the 90° bend and notch the sharper bend. At 56" cut away

the remaining bent metal leaving the rest as a tab for riveting. Now bend the piece 90° inward at each cut, and pop rivet (flat side in) the ends together and the inside flanges at two corners (to keep the tray from flexing). Complete the tray by drilling a $\frac{1}{4}$ " mounting hole at the midpoint of each lateral interior flange and riveting on an apron and side pieces made from a 6×24 " piece of $\frac{1}{4}$ "-mesh hardware cloth (Fig. 2B). Attach a tray to either end of the trap with $\frac{1}{4} \times 2$ " carriage bolts passing through holes drilled in the top piece. Carefully cut a slit in the netting and pull the netting over the apron. By bending the side pieces outward and the apron upward and by keeping the slit in the netting small, you can make a butterfly-tight seal between the tray and the netting. Repair any mishaps with silicon caulk.

Construct holding cages of $\frac{1}{4}$ "-mesh hardware cloth as described by Walker and Lenczewski (1989) ($11 \times 16 \times 10$ " with a valve in the bottom) (Fig. 2B). As an aid to servicing the cages, rivet a 3" piece of $1\frac{1}{4}$ "-diam PVC vertically to the top center of the back of each cage. Make a device for installing and removing cages from a 2 m length of $\frac{1}{2}$ " EMT with 4" and 11" crosspieces of $1\frac{1}{4}$ " PVC riveted at $3\frac{1}{2}$ " and 7" from the upper end (Fig. 1).

Securing the trap. Make stakes by cutting 18" lengths of $\frac{1}{2}$ " EMT. Near the top of each stake, drill a hole and install a bolt to prevent the stake from passing through a $\frac{3}{4}$ " eye. With the trap in position, thread each of its four inside eyes with a stake and drive each stake until the bolt reaches the eye.

GENERAL NOTES

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PARASITOIDS EXPLOIT SECRETIONS OF MYRMECOPHILOUS LYCAENID BUTTERFLY CATERPILLARS (LYCAENIDAE)

Additional key words: *Polyommatus*, Braconidae, Microgasterinae, ant-association, symbiosis.

Mutualistic interactions that are mediated by the delivery of nutritive material (e.g., nectar, pollen) bear the risk of being exploited by species of organisms outside of the mutualism. Numerous ant species, for example, maintain symbioses with plants bearing extrafloral nectaries (EFN's) or with sap-feeding Homoptera excreting honeydew. Specialized insects other than ants secondarily may utilize these energy-rich fluids (e.g., riodinid butterfly caterpillars: DeVries & Baker 1989; adult nepticulid moths: Downes 1968). Adults and larvae of Miletinae lycaenids induce ant-tended homopterans to release honeydew excretions via tactile stimulation (Maschwitz et al. 1988). In these and many more cases, the secondary beneficiaries of ant-plant or ant-homopteran mutualisms are adapted morphologically and/or behaviorally to overcome or avoid ant predation.

Supposedly mutualistic associations with ants also occur in a large number of species of the butterfly family Lycaenidae (e.g., Fiedler 1991). Myrmecophilous lycaenid caterpillars attract ants with the help of particular epidermal glands. One of these glands, the dorsal nectary organ (DNO), secretes carbohydrates and/or amino acids (Maschwitz et al. 1975; Pierce 1983). These nutritive secretions may cause ants to recruit nestmates to the caterpillars (Fiedler & Maschwitz 1989). In turn, the ants may provide protection against certain parasitoids or predators (e.g., Pierce et al. 1987).

DNO secretions usually are released only when ants antennate the immediate vicinity of this gland, which is equipped with specialized mechanosensory setae (Tautz & Fiedler 1992). Insects other than ants have been recorded to feed on DNO secretions only twice, i.e., thrips (Downey 1965) and Miletinae adults (Gilbert 1976). Here we describe a novel type of interaction: parasitoid wasps that feed on DNO secretions of their lycaenid host larvae.

In May 1991, nine caterpillars of *Polyommatus* (*Lysandra*) *coridon* (Poda 1761) were collected in southern France (Dep. Var. Grand Canyon du Verdon) under their hostplant, *Hippocrepis comosa* L. (Fabaceae). The larvae were attended by the Formicinae ant species *Plagiolepis pygmaea* (Latreille 1798). After 10 days in captivity, 8–12 braconid wasps emerged from each of four of the caterpillars. The braconid larvae soon pupated in silken cocoons attached to the cuticle of the dead caterpillars, and eight days later about 40 male and female wasps of an unidentified (and possibly undescribed) *Apanteles* species (subfamily Microgasterinae) eclosed in the morning (J. Papp & E. Haeselbarth pers. comm.; vouchers in coll. Hungarian Natural History Museum, Budapest).

On the following two days, five caterpillars of *Polyommatus* (*Meleageria*) *daphnis* ([Denis & Schiffermüller], 1775) and one pupa of *P. (Lysandra) bellargus* (Rottemburg, 1775) were offered to the adult parasitoids. Both these lycaenid species are closely related to the original host which was then no longer available as larva. In addition, all these lycaenids share the same hostplants in nature (*Coronilla* and *Hippocrepis* species).

When one large fourth (=final) instar caterpillar of *P. daphnis* was introduced into a plastic vial with 10 *Apanteles* wasps, a female braconid detected the caterpillar within less than 2 min, crawled back and forth on its dorsum and soon found the DNO. The wasp immediately started to antennate the DNO intensively and then repeatedly fed on the secretion droplets produced by the caterpillar. This association persisted for 20 min, when the wasp left the caterpillar without having parasitized it. Within 1 min another female wasp visited the same caterpillar and fed at the DNO, but again left it without ovipositing. A third female wasp at first antennated the DNO and received several

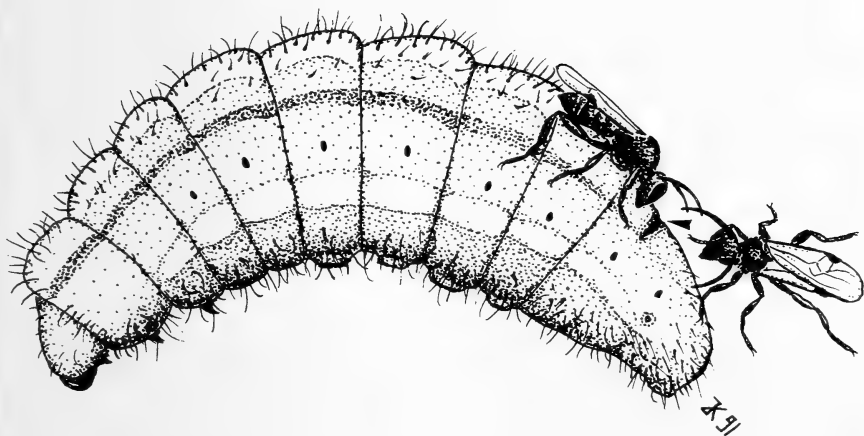


FIG. 1. Two *Apanteles* wasps visiting the DNO (arrow) of a final instar caterpillar of *Polyommatus daphnis*. Scale bar: 2.5 mm. Drawing by J. Klein after a photograph by K. G. Schurian.

secretion droplets, but stung the caterpillar after 6 min and laid one egg. Two further *P. daphnis* caterpillars subsequently were introduced to the same wasps; one was largely ignored while the other was parasitized within 5 min with no further feeding observed at the DNO.

When being stung, the caterpillars abruptly raised their heads and discharged fecal pellets as well as stomodeal regurgitations. However, these defensive behaviors typical of lycaenid caterpillars did not repel the parasitoids.

On the following day, two young fourth instars of *P. daphnis* were offered to the wasps, the latter having been starved for 24 h. Both caterpillars were immediately found by several wasps, and 2–3 braconids constantly elicited the release of carbohydrate secretions by antennating and even vigorously chewing at the DNO (Fig. 1). The wasps also intensively antennated the clusters of pore cupola organs (PCO's) which are situated around the larval spiracles. The PCO's are a second type of lycaenid myrmecophilous organs that are suspected to secrete amino acids (Pierce 1983). Within 1 h, three oviposition acts were observed, all of which were followed by long sequences of feeding at the DNO. During 4 h the caterpillars were continually visited and antennated by 2–3 wasps simultaneously. The wasps now rapidly found their way to the DNO, and few additional oviposition acts were observed.

The wasps were very effective in stimulating secretion acts from the DNO. Within 3 days, with daily observation periods of 1–3 h and about 10 parasitoids per trial, more than 100 secretion acts were observed directly, and all secretion droplets were licked up by the attendant wasps. The caterpillars also sometimes everted their tentacle organs (TO's) which are a third type of myrmecophilous organs in lycaenid larvae. Eversion of the TO's often induces a kind of alertness in attendant ants (Fiedler 1991). There was, however, no detectable effect of the TO's on the braconids. The ability of braconid wasps to release TO eversions is not surprising, since several lycaenid caterpillars also evert these organs when disturbed (Fiedler unpubl.).

Apanteles wasps likewise intensively antennated a pupa of *P. bellargus* and nibbled at it with their mandibles. The wasps' activities mainly concentrated at the pupal abdominal spiracles where dense clusters of the secretory PCO's occur. The wasps apparently harvested the PCO secretions. Larvae of *P. daphnis* were much more attractive to the wasps than was the pupa of *P. bellargus* throughout the trial (1 h).

Female braconids appeared to achieve significant benefits in terms of longevity from their secretion-feeding, while males with their generally short life-span did not. Ten females with no access to lycaenid caterpillars all died within 2 days, whereas 10 females that had fed repeatedly on the DNO secretions survived for at least 3 days. Feeding on homopteran honeydew and flower nectar has been demonstrated to increase both longevity and fecundity in certain braconid wasps (Hagley & Barber 1992). Male braconids were far less attracted to the caterpillars, and despite the presence of numerous male *Apanteles* wasps in the experimental arena, only once did we observe a male feeding on a secretion droplet. All males except this one died within one day.

An ichneumonid wasp, *Agrypon anomelas* (Gravenhorst) (det. H. Schnee), emerged from one of the remaining five *P. coridon* caterpillars. When brought into a vial with 3 fourth instar caterpillars of *P. daphnis*, this ichneumonid neither antennated the larvae intensively nor paid any particular attention to the DNO, despite the occurrence of numerous contacts between the wasp and the caterpillars. Another male ichneumonid randomly captured in the field (*Phygadeuon* sp., a dipteran parasitoid) likewise was unable to facilitate the release of any secretions from the myrmecophilous organs of two *P. daphnis* caterpillars. In both trials the ichneumonids showed little interest in the caterpillars.

In June 1992, we conducted similar trials with two additional Microgasterinae species (collected in the vicinity of Würzburg, northern Bavaria, Germany). *Distatrix sancus* (Nixon 1965) was obtained from field-collected larvae of the myrmecoxenous lycaenid *Callophrys rubi* (Linnaeus 1758). Ten females of this species were caged over night in a petri dish with 2 mature larvae of the highly myrmecophilous lycaenid species *Glauco-psyche alexis* (Poda 1761). Initially, the wasps paid little attention to the caterpillars, but on the following morning both caterpillars were visited by the wasps. Harvesting of DNO secretions occurred often, although the braconid-caterpillar associations were not truly permanent. There were no reactions towards the repeated eversions of the larval TO's, and the wasps did not try to sting the larvae. *Distatrix sancus* wasps caged with caterpillars of *G. alexis* survived for 2 days, but died within 24 h without this food resource.

We also tested *Cotesia cupreus* (Lyle 1925), a parasitoid reared from field-collected caterpillars of *G. alexis*. *Cotesia cupreus* wasps repeatedly stung mature *G. alexis* larvae, but never visited their DNO's in our trials. Again, defensive movements and TO eversions of the lycaenids failed to repel the parasitic wasps. When *C. cupreus* females were caged in petri dishes with mature caterpillars of *P. bellargus*, the wasps often stung these larvae, which again responded with defensive movements and TO eversions. For the most part, *C. cupreus* did not visit the DNO, but on one occasion two wasps antennated the DNO of mature larvae of *P. bellargus* and repeatedly harvested its secretions. *Mesochorus discitergus* (Say) (Ichneumonidae: Mesochorinae), a hyperparasitoid reared from *Distatrix sancus* (via *Callophrys rubi* caterpillars), never showed any interest in caterpillars of *G. alexis* or *P. bellargus*.

Although our observations were made under artificial conditions in the laboratory, they suggest that several parasitoids of the braconid subfamily Microgasterinae (*Apanteles* sp., *Distatrix sancus*, *Cotesia cupreus*) are able to use their lycaenid hosts in two ways: as a substrate for larval development and as a nutritive resource for the adult wasps. Given the amazing persistence of some wasp-caterpillar associations, feeding of DNO secretions probably occurs under natural conditions as well in female braconid parasitoids of myrmecophilous lycaenid larvae. The limited interest of male wasps in the caterpillar is not surprising given that males rarely, if ever, encounter host larvae in nature.

Several species of the braconid genus *Apanteles* are known parasitoids of myrmecophilous as well as myrmecoxenous lycaenid larvae (Dempster 1971; Pierce & Eastal 1986; Pierce et al. 1987). Unfortunately, little is known about the host-specificity and behavior of most of these lycaenid parasitoids. The *Apanteles* species reared from larvae of *P. coridon* was highly attracted to *P. daphnis* caterpillars as well as to a *P. bellargus* pupa. *Distatrix sancus* and *C. cupreus* wasps even visited the DNO of lycaenid larvae that belonged to different genera than their original hosts. Hence, the Microgasterinae species tested probably are not all species-specific parasitoids. That no *Apanteles* wasps emerged from the *P. daphnis* and *P. bellargus* caterpillars stung during our observations

can be attributed to the inadequate larval instar employed in our trials, i.e., *Apanteles* wasps usually parasitize younger instars.

Certain female braconids effectively mimic the tactile signals that ants normally use to elicit the DNO secretions of lycaenid caterpillars. Interestingly, the braconids resemble the ant species *Plagiolepis pygmaea* in size and overall activity pattern, and this ant species often tends caterpillars of *Polyommatus coridon* or *P. hispanus*. Because larvae of European *Polyommatus* and *Glaucopsyche* species are associated unspecifically and facultatively with a number of trophobiotic ant species from at least 8 genera in 3 subfamilies (Fiedler 1991), the signals required to release DNO secretions of such caterpillars cannot be highly specific. Indeed, secretion acts occasionally can be released artificially using vibrating hairs (Schurian unpubl.). However, because the ichneumonid wasps tested so far were unable to mimic the appropriate tactile signals, secretion-feeding of certain Microgasterinae wasps appears to be a peculiarity of these latter parasitoids.

Caterpillars of *Polyommatus coridon*, *P. hispanus*, *Glaucopsyche alexis* (all myrmecophiles) and *Callophrys rubi* (a myrmecoxenous species) suffer from parasitism by braconids, ichneumonids, and other parasitoids (this study; Schurian & Fiedler unpubl.), suggesting that the protective effect of tending ants is not perfect. In two other ant-caterpillar mutualisms, attendant ants have been found to be ineffective against parasitoids (Pierce et al. 1987; Nash 1989; DeVries 1991). Possibly, many parasitoids of myrmecophilous caterpillars are adapted to escape ant-attacks. In addition, the species of attendant ants, or the actual population densities of ants, trophobionts, and enemies, may influence the protective benefits of myrmecophily, as has been demonstrated for ant-homopteran interactions (e.g., Bristow 1984; Cushman & Whitham 1989). The attendant ants observed at the *P. coridon* larvae in southern France (*Plagiolepis pygmaea*) are among the smallest ant species of Europe and might thus yield particularly limited protection.

In the Australian lycaenid *Jalmenus evagoras* (Donovan 1805), braconids of the genus *Apanteles* have specialized on using the caterpillars' ant guard as an olfactory oviposition cue (Nash 1989). The larvae and pupae of all lycaenids involved in our experiments (*Polyommatus* spp., *Glaucopsyche alexis*, *Callophrys rubi*), as well as those of *J. evagoras*, produce substrate-borne vibratory signals. Such caterpillar "calls" might serve as additional cues in the host-locating behavior of some parasitoids. However, because all larvae of *G. alexis* or *C. rubi* that later yielded braconid parasitoids were collected as second instars, caterpillar vibrations appear to play no role as cue for parasitoids in the species tested here. The vibratory abilities of these lycaenid larvae commence with the third instar (Fiedler unpubl.).

Caterpillars of *C. rubi* and *G. alexis* retained their ability to produce vibratory signals even after the braconid larvae had emerged for pupation. In contrast, larvae of *C. rubi* parasitized by the tachinid fly *Aplomyia confinis* (Fallén 1820) lost their ability to vibrate a few days before the parasitoids left (Fiedler unpubl.). Clearly, the ecological and behavioral relationships between lycaenids, ants, and parasitoids merit further attention of lepidopterists, as evidenced by the discovery of the novel type of caterpillar-braconid interaction described here.

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EVIDENCE FOR USE OF WATER BALLAST BY MONARCH BUTTERFLIES, *DANAUS PLEXIPPUS* (NYMPHALIDAE)

Additional key words: migration, flight stability, gliding, soaring, lipids.

To ensure stable flight characteristics, the Center of Gravity (CG) of an aircraft must be located relatively close to the center of lift (Falk & Matteson 1971; Anonymous 1991). This constraint also applies to gliding butterflies. Gibo and Pallett (1979) investigated

aerodynamic characteristics of dried and weighted (i.e., ballasted with plasticine to a mass of 450 mg) *Danaus plexippus* L. (Nymphalidae: Danainae) and found that when the wings were set in the normal gliding configuration, stable flight was possible only if the CG was located slightly posterior to the metathorax. If the CG was ahead of this position, the butterflies pitched down into a dive; if behind, they pitched up, stalled, and fell (Gibo & Pallett unpubl. data).

Because *D. plexippus* usually migrate by soaring and gliding when conditions are favorable (Gibo 1986; Gibo & Pallett 1979; Schmidt-Koenig 1985), it seems reasonable that they must keep their CG close to the stable gliding position. Stabilizing the location of the CG may be a problem for the butterflies because each individual tends to accumulate more than 100 mg of lipid during the migration, most of which is deposited in the abdomen (Beall 1948; Walford 1980; Brown & Chippendale 1974; Gibo & McCurdy 1992). Unless the increase in lipid mass is compensated for, the CG's of the butterflies could shift into their abdomens, making the migrants less capable of stable gliding flight.

Loss of the ability to glide would be a serious handicap for migrating *D. plexippus*. Gibo and Pallett (1979) calculated that the butterflies had the capacity to glide for 1060 hours before depleting an average 140 mg lipid reserve, but would deplete it within only 44 hours if they migrated by cruising, flapping flight. Thus, flapping flight is approximately $1060/44 = 24$ times more costly than gliding and soaring flight. Other researchers have determined that flapping flight in *D. plexippus* can be 28 to 31 times more costly than gliding flight (Masters et al. 1988). Furthermore, even butterflies migrating primarily by flapping flight apparently reduce energy expenditures by alternating between bouts of flapping and gliding (Urquhart 1960). Considering that *D. plexippus* from eastern North America must migrate up to thousands of kilometers to overwintering sites in southern Mexico and must accumulate large lipid reserves along the way (Brower 1985; Masters et al. 1988), a significant reduction in the capacity for gliding flight would make it nearly impossible for the butterflies to succeed.

The butterflies could offset the effect of changes in lipid mass on the location of the CG by ballasting with water. If individuals with small lipid masses carried extra water in the abdomen, perhaps in their large crop, and eliminated it as lipid mass increased, they could keep their CG's at the optimal location. Surprisingly, the increased wing loading resulting from carrying extra water would tend to improve the gliding flight performance of the butterflies. An increase in wing loading raises gliding airspeed without changing the glide angle (Lighthill 1977; Piggott 1976; Welch et al. 1977). In other words, *D. plexippus* that carry ballast water are still able to glide as far as usual from a given height, approximately 3.5 m forward for every 1 m of descent (Gibo and Pallett 1979), but can fly faster. Because any increase in gliding airspeed allows the migrants to travel faster between thermals and to compensate for a greater range of crosswind and headwind conditions, butterflies with higher wing loading should be able to make faster progress towards the overwintering sites. Furthermore, if *D. plexippus* are adapted to glide most efficiently when carrying a moderate to large lipid mass, the normal condition for most of the migration (Beall 1948; Brown & Chippendale 1974; Cenedella 1971; Gibo & McCurdy 1992), then selection may have favored carrying extra water when lipid mass was small. Here we present evidence for the hypothesis that migrating monarchs use water as ballast to partially counteract the effects of changes in lipid mass.

Wet mass, dry mass, water mass, lean dry mass, and lipid mass were determined for 234 specimens collected over a period of 8 weeks during the late summer migration in southern Ontario, Canada. Specimens were collected on 19 different days from mid August to early October, in open fields on the Erindale campus of the University of Toronto in Mississauga, Ontario, Canada. Specimens were collected from mid-to-late afternoon, corresponding to the period when migration usually ends for the day and the butterflies descend to forage and locate roosting sites (Urquhart 1960; Gibo 1986). Specimens were netted and transferred to small polyethylene bags. Within minutes of capture, each bagged specimen was placed on crushed ice in an insulated box. They were then brought to the lab and stored at -16°C until analysis. To minimize evaporative water loss when determining wet mass, each specimen was weighed immediately after being removed from the freezer. Dry mass was determined after the specimen had been dried at 60°C for 24

TABLE 1. Means and standard errors of *D. plexippus* Lipid Mass/Lean Dry Mass (LM/LDM) ratios and Water Mass/Lean Dry Mass (WM/LDM) ratios for the three phases of the migration. Sample size = 234.

Phase of migration	N	Mean ratio \pm SE	
		LM/LDM	WM/LDM
Early	79	0.30 ± 0.01	1.54 ± 0.02
Middle	73	0.43 ± 0.02	1.44 ± 0.02
Late	82	0.23 ± 0.01	1.66 ± 0.02

hours. A standard protocol was used to measure lipid mass (Gibo & McCurdy 1992). Water mass was obtained for each specimen by subtracting dry mass from wet mass. Lean dry mass was obtained by subtracting lipid mass from dry mass.

A previous study showed that the migration in southern Ontario could be divided into 3 phases, an early phase (weeks 1–2 of the migration), a middle phase (weeks 3–4), and a late phase (weeks 5–8), and that median lipid mass peaked in the middle phase (Gibo & McCurdy 1992). If the butterflies were ballasting with water, then median water mass should show the opposite pattern and reach its minimum value in the middle phase of the migration. To control for size differences among individuals, Lipid Mass (LM) and Water Mass (WM) for each individual were expressed as ratios of the Lean Dry Mass (LDM). Thus, lipid mass ratios (LM/LDM) and water mass ratios (WM/LDM) were compared for different phases of the migration. The Kruskal-Wallis test (Stat View II 1991; Abacus Concepts, Inc., Berkeley, California, USA) was used to determine if the observed differences among the 3 groups were significant.

Table 1 shows that water mass ratio declined as lipid mass ratio increased, and increased

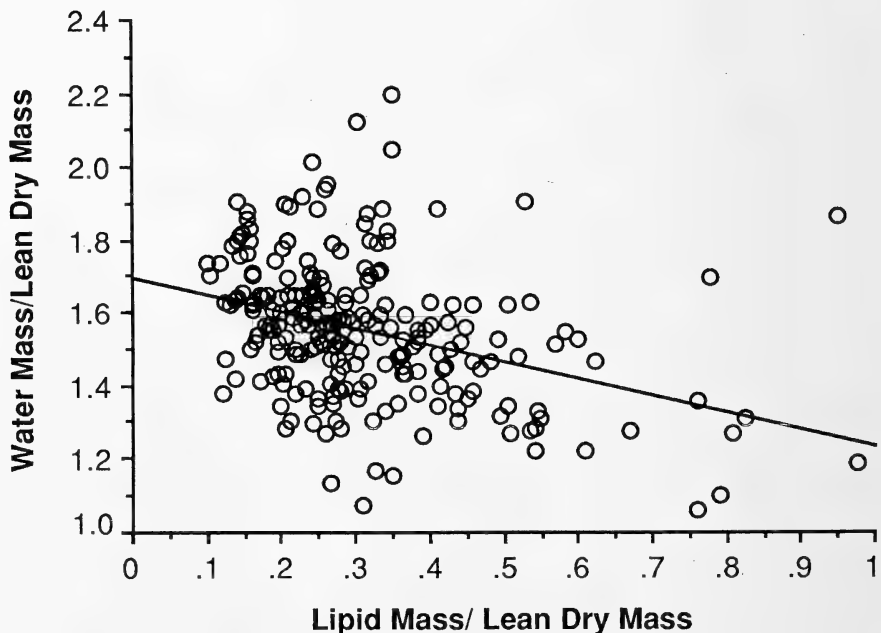


FIG. 1. Regression of *D. plexippus* lipid mass/lean dry mass (LM/LDM) ratios on water mass/lean dry mass (WM/LDM) ratios for the pooled data. Sample size = 254.

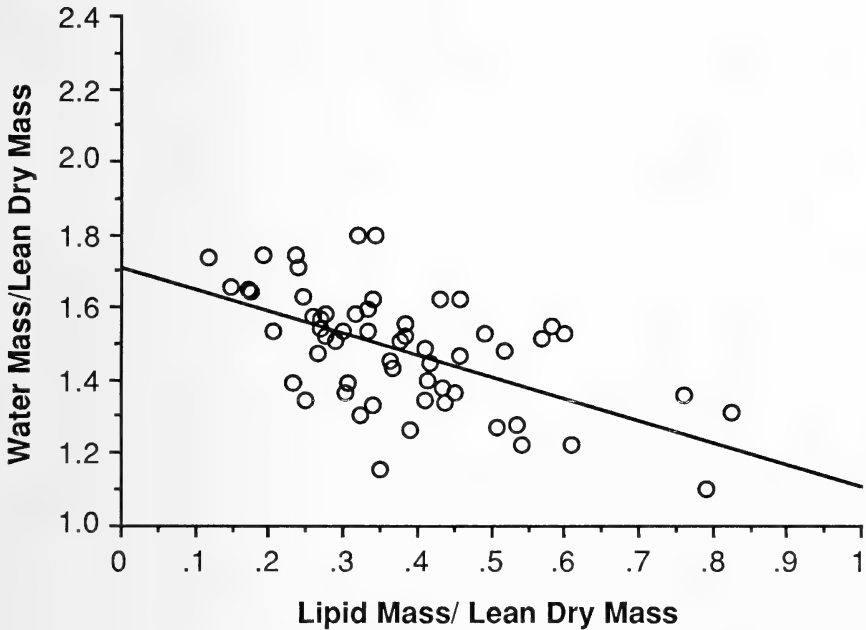


FIG. 2. Regression of *D. plexippus* lipid mass/lean dry mass (LM/LDM) ratios on water mass/lean dry mass (WM/LDM) ratios for the subgroup comprising the largest 25% of the specimens. All specimens in this subgroup had lean dry masses larger than 190 mg. Sample size = 59.

as lipid mass ratio decreased. As expected, maximum values for water mass ratio were observed in the early and late phases of the migration, while the value for lipid mass ratio peaked in the middle phase. The observed differences among the early, middle, and late lipid mass ratio groups were significant, with $n = 234$, $df = 2$, $H = 84.754$, and $P < 0.0001$. Observed differences among the early, middle, and late water mass ratio groups also were significant, with $n = 234$, $df = 2$, $H = 46.406$, and $P < 0.0001$.

Simple linear regression was used to model the relation between water mass ratio and lipid mass ratio for the pooled data ($n = 234$) and for a subgroup ($n = 59$) comprising the 25% of individuals with the greatest lean dry mass (i.e., >190 mg). The subgroup of large butterflies was analyzed separately because larger individuals are more likely to have difficulties stabilizing their CG with changes in lipid mass owing to the longer lever arm between the posterior of the metathorax and the center of mass for the abdomen. The large butterfly subgroup had a mean lipid mass ratio of 0.38 ± 0.02 and a mean water mass ratio of 1.48 ± 0.02 . Figures 1 and 2 show that there was an inverse relationship between water mass ratio and lipid mass ratio for both the pooled data and the large butterfly subgroup. The regression was significant in each case, with $n = 234$, $b = -0.46$, $df = 1/232$, $F = 35.05$, $P < 0.0001$ for the pooled data, and $n = 59$, $b = -0.60$, $df = 1/57$, $F = 27.61$, $P < 0.0001$ for the large butterfly subgroup. The 95% confidence intervals for the slope were -0.31 and -0.62 for the pooled data and -0.37 and -0.84 for the large butterfly subgroup. Regression coefficients were 0.36 for the pooled data and 0.57 for the large butterfly subgroup. Consequently, the regression accounted for just 13% of the total variance observed for the pooled data and 33% of the variance for the large butterfly subgroup. As expected, the inverse relationship between lipid mass ratio and water mass ratio was stronger for larger individuals.

If migrating *D. plexippus* use water as ballast, then an increase in lipid mass is not matched by an equivalent decrease in water mass. Both the regression equation for the population ($Y = -0.46X + 1.70$) and for the subgroup of large butterflies ($Y = -0.60X + 1.71$), indicate that for each 1.0 mg gain in lipid mass, the butterflies lost, on average, approximately 0.5 mg of water, and vice versa. In each case, the impact of changes in lipid mass on the location of the CG would have been reduced but not eliminated. With each gain or loss in lipid mass, the CG tended to shift about 50% of the distance that it would have moved if elimination or uptake of water had not occurred.

One possibility that should be considered is that ballasting may occur, in part, as an automatic consequence of nectaring, particularly if nectar is stored in the crop and the amount of expansion of the crop is largely determined by lipid mass. This is particularly likely to have been the case for the early and middle phases of the migration, from mid August to mid September, when conditions were favorable for the butterflies (Gibo & McCurdy 1992). However, during the late phase of the migration, from mid September to early October, weather conditions deteriorated. This period was characterized by frosts, a reduction in the amount of time that maximum daytime temperatures were above the flight threshold of the butterflies, and an increased frequency of periods of rain and overcast sky (Gibo & McCurdy 1992). As a result, late phase migrants, apparently experiencing a reduction in opportunities to forage and, perhaps, in availability of nectar, quickly lost lipid mass (Gibo & McCurdy 1992). Although late phase migrants may have accumulated their extra water mass through foraging and ingesting large amounts of presumably low quality nectar (the butterflies were losing lipid mass), drinking water from puddles and wet vegetation seems a more likely mechanism.

It is interesting to consider how partial ballasting would affect the aerodynamics of *D. plexippus*, particularly when compared to the effects of alternate methods of adjusting the location of the CG. Assuming that butterflies with small lipid masses achieve aerodynamic balance by carrying extra water as ballast, then their total mass will increase as lipid mass increases, although at a slower rate because of elimination of ballast water. As wing loading increases, their CGs will be shifted posterior to the stable gliding position. However, by sliding their forewings back over the hind wings, the butterflies should be able to move their centers of lift sufficiently close to their CGs to produce a new stable gliding configuration. Because this maneuver also reduces wing area, wing loading will increase faster than total mass and should result in a deterioration in flight performance. Although the combination of greater wing loading and reduced wing area should increase the gliding airspeed, it also should increase both the stall speed and the rate of sink as well as steepening the glide angle. Although the migrants would be able to glide faster between thermals, they would not be able to glide as far and would descend at a faster rate. Overall, these changes reduce the ability of the butterflies to soar cross-country and increase energy expenditures for flapping flight. Consequently, even with ballasting, migration should be more costly for *D. plexippus* with large lipid reserves. Presumably, increased costs of transport are offset by an increased probability of survival once the butterflies reach the overwintering sites.

Other methods of adjusting the CG that do not involve partial ballasting are feasible, but would either prevent the butterflies from enhancing their flight performance through higher wing loading or would lower flight performance. One method would be for *D. plexippus* with small lipid masses and CG's located anterior of the stable gliding position to slide their forewings forward. This maneuver would shift the center of lift sufficiently close to CG to produce a stable gliding configuration. However, because this maneuver increases wing area, it also increases drag and reduces flight performance. Gibo and Pallett (1979) found that a swept forward wing configuration resulting in an approximately 20% increase in wing area was associated with a 40% reduction in gliding airspeed and a steeper glide angle. Butterflies with wings swept forward should not be able to fly as fast, glide as far, or compensate for as great a range of unfavorable winds, as those that maintain the standard wing configuration and adjust their CG with ballast water. On the other hand, migrants could adjust their CG without changes in wing configuration by either extending the abdomen or by inflating their crop with air to push their internal organs to the posterior of the abdomen. However, they would not achieve the increased

gliding flight performance associated with greater wing loading. Finally, monarchs with large lipid masses that did not eliminate water, but simply bent their abdomen up or down to bring the center of mass closer to the center of lift, also should experience a deterioration in flight performance. The bent abdomen would protrude into the airflow, resulting in increased drag and a tendency to pitch the butterfly up or down, depending upon whether it is held above or below the wings. The increased drag would result in a steeper glide angle, an increased rate of sink, and a lower airspeed, while the pitching moment may make stable gliding flight impossible without further compensatory changes in wing configuration. Although these other methods may be used, carrying water ballast seems to be the most effective means for migrating *D. plexippus* to adjust the position of their CG to compensate for changes in lipid mass, particularly since the resulting increase in wing loading should enhance flight performance. Nevertheless, because our evidence is correlative, ballasting by migrating *D. plexippus* in response to changes in CG remains a hypothesis. Finally, since gliding and soaring flight have been reported for other migratory insects, including *Nymphalis antiopa* L. (Nymphalidae) (Gibo 1981b), *Vanessa cardui* L. (Nymphalidae) (Myres 1985), six members of the odonate genera *Tramea* and *Pantala* in the family Libellulidae (Gibo 1981a; Walker & Corbet 1975), and the desert locust *Schistocerca gregaria* Forsk (Acrididae) (Roffey 1963), these species also should be considered candidates for employing ballast to adjust their CG.

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NOTES ON *DANAUS GILIPPUS STRIGOSUS* (NYMPHALIDAE: DANAINAE) IN SOUTHERN CALIFORNIA

Additional key words: Asclepiadaceae, *Asclepias*, milkweed, host plant, distribution, striated queen.

The striated queen, *Danaus gilippus strigosus* (Bates), is a widespread butterfly that breeds throughout much of southwestern United States and northwestern Mexico (Howe 1975); it is common throughout the Colorado Desert in California (Emmel & Emmel 1973). Although adults are found regularly along the Pacific coast of California from Santa Barbara to San Diego and in the adjacent coastal mountains during autumn of most years (Coolidge 1926; Emmel & Emmel 1973), they are considerably less common in the coastal region during the spring and summer (e.g., Orsak 1977). Most late summer and fall records of this species from the coast likely represent adults that have dispersed from the desert; however, some small populations may be established in coastal San Diego County (e.g., Mission Gorge, Otay River Valley) or elsewhere where larval hosts are available (J. Brown pers. comm.). The purposes of this note are to present records of new larval hosts and document the colonization by *D. gilippus* of the coastal region of southern California.

Coolidge (1926) and Emmel and Emmel (1973) reported climbing milkweed, *Sarcostemma hirtellum* (R. Holm) (Asclepiadaceae), as the primary larval host of *D. gilippus* in the desert areas of southern California, and Emmel and Emmel (1973) suggested that purple climbing milkweed, *Sarcostemma cyanooides* ssp. *hartwegii* (R. Holm), may be used as well. Emmel and Emmel (1973) also reported that larvae of *D. gilippus* have been taken on *Asclepias albicans* (Wats.) and *A. erosa* (Torr.), both of which occur in the Colorado Desert (Munz 1974). Comstock (1927) and Coolidge (1926) reported intro-

duced oleander (*Nerium* sp.) (Apocynaceae) as a larval host plant, but it is highly unlikely that oleander is used on a regular basis.

I collected a single larva of *D. gilippus* on *Asclepias fascicularis* (Dcne.) at each of two locations: 1) near Fort Tejon State Historic Park in the Tehachapi Mountains, Kern County (18 September 1988); and 2) Leo Carrillo State Beach at the western edge of the Santa Monica Mountains about 100 m from the coast, Los Angeles County (2 October 1988). Both larvae were reared to adulthood on their original host plants. The specimens are in the collection of the author. Larvae of the monarch butterfly (*Danaus plexippus* L.) are found regularly in the fall feeding on *A. fascicularis* at both of these localities.

David Marriott (pers. comm.) observed a last instar larva of *D. gilippus* on the introduced *Asclepias curvassavica* (L.) near Encinitas in coastal San Diego County (November 1991). He also reported observations (by Maureen Calvert) of pupae on *A. curvassavica* and adults ovipositing on this species in this area for 8 years. Marriott also reported observations (by Tony Leigh) of a last instar larva of *D. gilippus* on *A. fascicularis* at Harbor Lake Regional Park, Harbor City, Los Angeles County (23 September 1984).

In southern California, *D. gilippus* probably is a permanent resident only in the Colorado Desert. Based on host plant availability and observations presented above, this species may occasionally colonize coastal or montane areas following late summer or fall dispersal. The duration of coastal residency may be determined by low temperatures and host plant availability in winter.

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SEASONAL AND FOODPLANT-DETERMINED DIFFERENCES IN
PRODUCTIVITY AND REPRODUCTIVE SUCCESS OF THE INDIAN
TASAR SILK MOTH, *ANTHRAEA MYLITTA* (SATURNIIDAE)

Additional key words: emergence, polyphagous, *Terminalia tomentosa*, *Terminalia arjun*, *Shorea robusta*.

The Indian tasar silk moth, *Antheraea mylitta* (Drury), is a semi-domesticated species used in silk production. It is polyphagous and is reared commercially during three seasons per year: (1) rainy season (July–August), (2) autumn (September–October), and (3) winter (November–December). Seasonal factors and foodplants have considerable influence on the life cycle of other silk producing species. Joshi (1985) reported that the type of larval foodplant affects fecundity of the eri silk moth, *Philosamia ricini* Hutt. (Saturniidae), and Bari and Islam (1985) observed that different varieties of mulberry influence cocoon weight and fecundity of the mulberry silk moth, *Bombyx mori* L. (Bombycidae). Owing to the economic importance of *Antheraea mylitta* in India, information on these features as they relate to the productivity and reproductive success of the tasar silk moth are of considerable importance. Hence, we conducted experiments to evaluate the effects of larval foodplant and rearing season on *A. mylitta*. We report on percent emergence, percent coupling success, fecundity, and percent egg hatching of *A. mylitta* reared on three different foodplants—asan (*Terminalia tomentosa* Wt. & Arn., Combretaceae), arjun (*Terminalia arjuna* Wt. & Arn., Combretaceae), and sal (*Shorea robusta* Gaertn, Dipterocarpaceae)—during three rearing seasons.

Five thousand cocoons of *A. mylitta* were collected at random from each of three different foodplant lots at the Tasar Research Farm, Durgapur, Orissa, India. Each batch of 5000 cocoons was divided into five replicates, each containing 1000 cocoons. The replicates were kept in the grainage, a house specially designed for storage of cocoons, for observations. Percent emergence of adults, percent coupling success, fecundity, and percent hatching of subsequent eggs were noted. The experiment was repeated in each of the three rearing seasons in 1988 (i.e., rainy, autumn, and winter) for each of the three hostplants. The differences in mean values for each of the four parameters studied were analyzed statistically using Student's *t*-test (Snedecor & Cochran 1967). The results of the rearing experiments are presented in Table 1.

Percent cocoon emergence. Larvae reared on asan and arjun during autumn exhibited the highest percent cocoon emergence, 94.4 and 90.5% respectively. In general, percent cocoon emergence was highest in autumn, second highest in the rainy season, and lowest in winter. None of the foodplants tested produced the highest percent emergence in all three seasons.

Percent coupling success. Highest percent coupling success was achieved during the autumn rearing season by moths reared on asan (87.8%). Second highest also was achieved during the autumn, by moths reared on arjun (80.5%). In general, greater coupling success occurred in the autumn generation, second highest in the rainy season, and lowest in winter. Moths reared on asan had the highest coupling success in each season; those reared on arjun exhibited the second highest percent in each season, and those on sal the lowest.

Fecundity. Number of eggs laid per female was highest in the winter by females reared on sal (220.8 eggs/female). Second highest fecundity was achieved in the autumn season by females reared on sal (215.7 eggs/female). In general, fecundity was highest in the winter, second highest in autumn, and lowest in the rainy season. For the foodplants tested, moths raised on sal consistently produced the greatest number of eggs, regardless of rearing season; those on asan produced the second highest, and those on arjun the lowest.

Percent hatching. Eggs from females of the winter generation reared on asan had the highest percent of egg hatching (86.8%). Eggs from females of the autumn generation reared on asan had the second highest percent egg hatching (81.2%). In general, percent egg hatching was highest during the winter generation, second highest in the autumn generation, and lowest in the rainy season generation. Eggs from females reared on asan consistently produced the highest percent hatching regardless of the season; eggs from

TABLE 1. Mean percent emergence, percent coupling success, fecundity, and percent egg hatching of *A. mylitta* reared on asan, arjun and sal in three different seasons.

Season	Food plant	Mean percent emergence (\pm standard deviation)	Mean percent coupling success	Mean number of eggs laid per female (fecundity)	Mean percent egg hatching
Rainy	Asan	75.23 \pm 15.48	68.34 \pm 10.41	195.73 \pm 26.54	77.65 \pm 3.84
	Arjun	66.42 \pm 1.78	63.68 \pm 12.14	174.43 \pm 32.37	72.31 \pm 5.63
	Sal	78.67 \pm 16.83	55.42 \pm 10.43	208.47 \pm 2.67	71.46 \pm 4.41
Autumn	Asan	90.37 \pm 6.66	87.82 \pm 5.74	198.87 \pm 10.85	81.18 \pm 2.67
	Arjun	90.54 \pm 8.36	80.50 \pm 8.64	185.76 \pm 15.84	77.62 \pm 3.82
	Sal	80.74 \pm 8.44	60.62 \pm 7.46	215.75 \pm 26.75	75.73 \pm 2.27
Winter	Asan	70.49 \pm 8.32	65.33 \pm 8.32	205.66 \pm 10.54	86.77 \pm 2.46
	Arjun	63.67 \pm 9.46	60.54 \pm 9.53	200.05 \pm 11.76	80.71 \pm 4.66
	Sal	55.62 \pm 9.62	42.40 \pm 8.52	220.84 \pm 20.35	76.46 \pm 2.84

females reared on arjun achieved the second highest percent hatching, and those raised on sal lowest.

The probability values ($P < 0.05$) of *t*-tests demonstrated a statistically significant difference in percent emergence, percent coupling success, and percent egg hatching among the rearing seasons, irrespective of host. The difference in mean fecundity among generations was not statistically significant.

Analysis by foodplant type showed that the highest percent emergence, percent coupling success, and percent egg hatching were achieved by cocoons from asan, followed by those from arjun and sal plants. The highest average fecundity was achieved by cocoons from sal, followed by those from asan and arjun. The probability values ($P < 0.05$) of *t*-tests showed a statistically significant difference in percent emergence, percent coupling success, fecundity, and percent egg hatching of *A. mylitta* reared on different foodplants during the autumn and winter seasons. However, differences were not statistically significant for these parameters on different hosts during the rainy season.

Opende and Tikku (1979), Sharma and Badan (1986), Govindan and Magadum (1987), and Haniiffa and Punitham (1988) all reported that the variety of mulberry used has considerable influence upon fecundity and cocoon weight in the mulberry silk moth, *Bombyx mori*. Our studies demonstrate that significantly different percent emergence, percent coupling success, and percent egg hatching can be achieved by *A. mylitta* during different seasons; and significantly different percent emergence, percent coupling success, fecundity, and percent egg hatching can be achieved by rearing *A. mylitta* on different foodplants during the autumn and winter generations.

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BOOK REVIEWS

THE LEPIDOPTERA OF BERMUDA: THEIR FOOD PLANTS, BIOGEOGRAPHY, AND MEANS OF DISPERSAL, by D. C. Ferguson, D. J. Hilburn, and B. Wright. 1991. Memoirs of The Entomological Society of Canada, No. 158. Soft cover, 16.5 × 25.5 cm, 105 pp., 1 color frontispiece, 204 black and white figures. ISSN 0071-075X. Available from The Entomological Society of Canada, 393 Winston Avenue, Ottawa, Ontario, K2A 1Y8, Canada. Price in Canada: \$15 (Canadian) non-members, \$12 members of ESC. Price in U.S.A.: \$13.50 (U.S.) non-members, \$10.75 members of ESC. (All prices postpaid.)

The authors of this monograph and A. B. Ewen, current Editor of the Memoirs, are to be congratulated on a most professional production. The basic content is a systematic treatment of the 183 species of Lepidoptera recorded from Bermuda, arranged in the sequence of the *Check List of the Lepidoptera of American North of Mexico* (Hodges et al. 1983, E. W. Classey Ltd., Faringdon, England, and the Wedge Entomol. Found., Washington, D.C.), with some modifications where more recent published taxonomic changes have been accepted. Following a brief introduction are concise descriptions of the natural history and physiography of Bermuda and historical notes on the early collectors and students of the Lepidoptera of Bermuda. A separate section evaluates dubious historical records and explains why certain species are excluded from the check list that follows, in which each species is identified as endemic, migratory but presently established, irregular visitor, accidentally introduced, or of uncertain status. An interesting and thought-provoking essay by Ferguson on migration of Lepidoptera, with special reference to the history and establishment of the fauna of Bermuda, is included as an appendix. It is accompanied by a table that lists Lepidoptera known to migrate regularly in eastern North America, with notes to indicate which of these species also reach Bermuda. All but the common butterflies and the larger, showier moths are well illustrated by 201 black and white photographs grouped near the end of the volume and followed by an index of scientific names. Errors and synonyms discovered in earlier accounts are clearly identified. The volume is not expensive and should accompany any entomologist visiting Bermuda. It can also be of assistance in identifying quite a number of the more common noctuids and pyralids found in the eastern United States.

This monograph is the most thorough and comprehensive treatment of the fauna of these islands. It is also the first review of the Lepidoptera of Bermuda since L. Ogilvie provided a check list of over 100 names in his "Insects of Bermuda" in 1928. I hasten to say that Mem. Entomol. Soc. Canada No. 158 not only will be the standard reference work on Bermudian Lepidoptera for many years to come, but also far exceeds in content the minimum requirements for a reliable, regional systematic review. As mentioned above, the authors have included fascinating historical information concerning not only the contributions made by the early collectors, but also the legacy of problems left by some early workers, e.g., the Reverend H. B. Tristram, who attached names to Bermudian Lepidoptera based only on experience with butterflies and moths of England. (This would not have mattered much had not several later authors perpetuated these erroneous records by taking them at face value.) Also included is much useful botanical, geological, and biogeographical information on Bermuda.

This volume is of considerable interest to me. I visited Bermuda first in 1976 and again in 1982 on other business, but between fruitless searches in rough seas for the humpback whales reported off Bermuda by Roger Payne and Scott McVay in the early 1970's, I managed to do some limited collecting for Lepidoptera in Sandys and Warwick parishes. The results of the first night convinced me that there was an awful lot of *Spodoptera* spp. in this manicured paradise!

After a few more days, however, I became impressed by the number of species recorded, if not by their exotic qualities or rarity. This point is stressed by Ferguson et al.: Bermuda has a supersaturated lepidopterous fauna, the result of frequent pulses of migrants from the southeastern seaboard of North America and the eastern Caribbean. Ferguson comments that years ago he saw the potential of Bermuda as an insular field laboratory to test hypotheses on dispersal and migration of Lepidoptera. There is no evidence to suggest

that the islands of Bermuda received any of their resident fauna and flora by previous links to the mainland, so, mercifully, a digression concerning the protracted conflict between dispersalist and vicariance biogeographers can be avoided in this case.

The small cluster of islands called Bermuda sits on the crest of a marine volcano uplift of probable Oligocene age, and there has been some land in the present area for perhaps up to one million years. No doubt, founder effect has played a continual role in the establishment of species of plants and animals throughout the Pleistocene and Recent history of Bermuda, with periodic evolution of endemism. There have been rather irregular, cyclic changes in altitude and exposed surface area during the Pleistocene, sometimes increasing the exposed land and reef area to between 600–700 km², at other times reducing it to perhaps less than 10 km². The present surface area is about 54 km². Each sea level change was almost certainly accompanied by significant alteration in mean annual air temperature and rainfall. Such oscillations frequently are inimical to flora and fauna alike. Nevertheless, some groups manage to survive such vicissitudes, and a few species may even prosper during unstable periods. The long-term result, however, has been periodic extinction of endemic elements, particularly those with specialized food plants and habitat requirements or restricted ranges. The current faunal association of Lepidoptera (one hesitates to call it a “community”) on Bermuda, then, is comprised mostly of immigrants, many of relatively recent origin. Historical data indicate that some species of the genus *Spodoptera*, for example, of which I wrote so slightly earlier, were not known to entomologists working on Bermuda 20–80 years ago. Occasional transients, which are recorded in each observational season, comprise a category of species that has yet to demonstrate a capacity to breed successfully on Bermuda for an extended period.

Only 15,000 years after the last glacial stadial and 6,000 years after the “warm” period, Bermuda has but a handful of endemic Lepidoptera. Ferguson et al. conclude that these endemic Lepidoptera—11 species and 2 subspecies—are those that survived the last drastic reduction of land area, somewhat over 100,000 years ago. Each time such cyclic events occur, there is presumably a dramatic reduction in diversity. During the relatively long intervening periods of stability, however, biodiversity of any group should attain some kind of equilibrium related to the limited surface area and food plant resources available. During such stability plateaux the chances of new immigrant Lepidoptera establishing themselves as permanent residents presumably might be much reduced. Success is perhaps at a maximum shortly after the occurrence of climatic events unfavorable to the endemic populations. However, this does not imply that the number of species on Bermuda at any given time in the past necessarily would have been lower than today; there would still have been annual influxes of transients from the southeastern seaboard of North America, and from the eastern Caribbean, except in times when there were major changes in the flow of the Gulf Stream and North Atlantic Drift and their associated air masses. However, these immigrant waves may have consisted of quite different species of Lepidoptera than those that have established themselves in relatively recent years.

In his essay on migration, Ferguson argues that even in the case of the cutworm pest species and their allies, most of the lepidopterous fauna of Bermuda was not introduced by man, but became established after over-water dispersal from southeastern North America, and the northeastern Caribbean islands. The greater numbers of cutworms and other noctuids taken in traps today, as compared to the numbers recorded by early collectors on Bermuda, are attributed to these migrants being less abundant in the past. Ferguson concludes that the great agricultural modification of southeastern North America during the last century, with the substitution of arable land for forests, provided and sustained conditions for a huge increase in population sizes of such species that thrive not only on crops but also on the large tracts of weedy fallow land that accompany forest clearing and agriculture.

Similarly, massive disturbances inflicted on the New Zealand flora and fauna by humans have facilitated the establishment of more migrant Lepidoptera, especially from Australia, in the last 50 years or so than in the entire period when E. Meyrick (1887, *Trans. Proc. N.Z. Inst.* 19:3–40), A. Philpott (1928, *Trans. Proc. N.Z. Inst.* 58:359–370), G. V. Hudson (1928, *The butterflies and moths of New Zealand*, Ferguson and Osborn Ltd., Wellington,

N.Z.), and others were recording and describing the Lepidoptera of the archipelago. Data collected by K. J. Fox (1975, *N.Z. Entomol.* 6:66–69) at traps set up at Cape Egmont on the west coast of the North Island for example, suggest that in most years the jet streams carry migrants to New Zealand in far greater abundance than was believed in earlier years. Although historically this probably has been a continual process, establishment may have been more difficult during relatively long periods of ecological stability prior to the arrival of humans within the last one thousand years. The original flora of New Zealand had such a large proportion of endemic groups that suitable foodplants for most Australian insect species were simply absent. Even when light seed was windblown or carried by birds, the germinating plants would still be prone to competitive exclusion by established floral communities.

At this point, it is worth pausing to see what Ferguson et al. have to say about the ecology of Bermuda, if in fact one can glorify Bermuda with that term. In many ways present-day Bermuda resembles the huge, disturbed, urban fringe areas of North America, where remnants of the native vegetation are inextricably mixed with introductions from other North American life zones and from every part of the world. Programs to conserve or enhance biodiversity of native insects in stressed, degraded, and often polluted environments face the same basic problems whether the habitat is an oceanic island or a continental region.

The majority of the plant species that comprised the Bermudian flora when the islands were discovered still survive today. These include 17 endemic species, which range in size from Bermuda Moss (*Trichostomum bermudanum*) to Bermuda cedar (*Juniperus bermudiana*). The ecological communities, however, are gone beyond reclamation. They have been lost to agricultural clearing, periodic burning, early demand for building timber and firewood, and, in the case of the relict native cedar groves, the depredations of an introduced scale insect which brought the tree to the brink of extinction. Ferguson et al. note that the surviving endemic plants face intense competition for resources from introduced weed species of a wide taxonomic range. Similarly, the insect fauna is now dominated by pest species of various kinds that develop large populations periodically, particularly on island crops and introduced horticultural species which now abound in gardens, hotel grounds, and golf courses. The authors also believe that a geometrid moth *Semiothisa ochrifascia*, which fed only on Bermuda Cedar, is now extinct, since the last confirmed capture was in 1928.

In many respects the ecological problems of Bermuda resemble, only too well, those of many other oceanic islands in the tropics and subtropics—such as Fiji, Tonga, Samoa, Easter Island, St. Kitts, the Caymans, Guam, Hawaii—the list is depressingly long. In 1973, F. A. Fosberg (pp. 209–215, in *Nature Conservation in the Pacific*, A. B. Costin and R. H. Groves (eds.) Austral. Nat. Univ. Press, Canberra) published a special plea for a world program to try to save the unique floras and faunas of oceanic islands. There has been some progress since then, in Madagascar, Aldabra and Jamaica, for example, but the total effort is still pitifully limited. Bermuda is particularly vulnerable because of its small size, accessible topography, attractive climate, and proximity to major population centers of eastern North America.

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REARING WILD SILKMOths, by Ronald N. Baxter (with a foreword by Brian O. C. Gardiner). 1992. Chudleigh Publishing, 45 Chudleigh Crescent, Seven Kings, Ilford, Essex IG3 9AT, England. x + 72 pp., 2 black & white pls., 8 text figs., 28 color photos by the author. Soft cover, 14.75 × 21 cm, ISBN-0-9519219-0-8, £7.95, plus £2.20 for airmail. (U.S.A. buyers can send \$20.00 in cash to receive one copy by airmail.)

Because members of the Saturniidae are the most popular Lepidoptera for rearing and because many amateurs list this family as their specialty, I assume this book will have a good market. It may fill a need for those wishing to rear saturniids who are unaware of, or unable to obtain, out-of-print books like Paul Villiard's *Moths and How to Rear Them* (1969, Funk & Wagnalls and 1975, Dover Reprint) or B. O. C. Gardiner's *A Silkworm Rearer's Handbook* (1982, Amateur Entomol. Soc.). Baxter's new book appears to be targeted almost exclusively for a British audience, but as many American and European writers similarly limit their scope to within their own borders, people in other countries are by now quite accustomed to this approach.

The color photographs on the front and back covers and the twenty inside showing live moths are superb and comprise the most attractive feature of the book. In addition there are eight color photographs of mature larvae, that although not glossy, are clear and crisp. For several species these are the only published photographs I have seen of live adults and larvae. Baxter is an accomplished photographer, both in technical quality and composition. I particularly liked to see moths of species that overwinter as eggs shown on autumn foliage. Baxter's illustrations are comparable to those of Hsiao Yue Wang of the Taiwan Museum, who in my opinion is the foremost photographer of moths in the world today. The photographs in Baxter's book alone make it worth the price.

The organization of the book is good, and the writing style makes the text easy to understand. Brief chapters dealing with care of eggs, larvae, pupae, cocoons, and adults; mating of moths; and how to obtain breeding stock are instructive, and will be especially useful to beginners. Of special value are the detailed treatments of the rearing needs of 42 silkworm species, of which 35 belong to the subfamily Saturniinae. Typographical errors and misspellings are rare in the book.

I disagree with a few comments made by the author, such as his generalization that tender young leaves are harmful to larvae (they rarely are; it all depends on the species of moth and plant). Wetting eggs is virtually always beneficial, particularly for diapausing ova, as long as ventilation prevents molding, yet Baxter advocates letting only indirect moisture reach eggs in their hatching containers. Baxter laments that "*Antheraea*" *eucalypti* can be reared only on eucalypts, not easily available in Britain, yet New Zealand entomologists have found the larvae in recent years on other resiniferous trees such as sweetgum, sumac, and even birch. The moth figured in color as *Rothschildia jorulla* is actually *R. cincta*. The specimen figured in color as *Automeris coresus* appears to be *A. rubrescens*. And intergeneric matings do, in fact, sometimes result in fertile ova.

Despite what Baxter writes, Shantung silk is no longer the correct name for that produced by *Antheraea pernyi* (although apparently this name caught on at some point in the past), nor is the center of its production in Shantung Province (now called Shandong). For several decades now the name Shantung silk has been applied to a category of mulberry silk (from *Bombyx mori*), which I see in profusion in fabric shops in Denver. The tussah silk industry in China has been centered in Liaoning Province for at least two centuries (and provided 70% of China's output of tussah in 1980, for example), but this oak silk is now grown throughout most of China. So much for the "association" between the province and name Shantung and Chinese tussah silk.

As a taxonomist I can only express frustration to see some long-standing errors in nomenclature perpetuated. The author should have consulted current taxonomically sound literature or requested editorial input from someone who could correct the following errors. The splendid giant moth from the Himalayas called *edwardsii* (Baxter uses the frequent misspelling *edwardsi*) belongs in *Archaeoattacus* (since 1910!), not *Attacus*. *Leucanella memusae* is still placed (erroneously) in *Automeris*, and, if Baxter has it identified correctly, does not occur in Argentina. The International Code on Zoological Nomenclature (1985) states categorically that junior objective synonyms are unavailable names and cannot be used: *Dictyoploca* and *Caligula* both have *simla* as type-species, and the latter generic name has priority; *Philosamia* and *Samia* both have *cynthia* as type-species, and again *Samia* is the older name. Even so, dozens of authors in Europe, Japan, China, India, and North America continue to use names like *Philosamia*, so Baxter has abundant company. The incorrect subfamily name Citheroniinae continues to be used

for the group correctly called *Ceratocampinae*. Then we find the usual dogma of putting the Australian *eucalypti* into *Antheraea* instead of *Opodiphthera*, and citing all of the species of *Samia* as subspecies of *cynthia*. The wheels of taxonomy grind painfully slowly!

I recommend this attractive little book for its helpful advice in rearing the big moths, and for its excellent color photographs of them, even though the price seems a bit high to me.

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BUTTERFLIES OF BORNEO, Volume II, No. 1: LYCAENIDAE, by Yasuo Seki, Yusuke Takana-mi, Kiyoshi Maruyama, and Kazuhisa Otsuka. Volume II, No. 2: HESPERIIDAE, by Kiyoshi Maruyama, and Addendum of Vol. 1, by Kazuhisa Otsuka. 1991. Tobishina Corporation, 2, Sandan-cho, Chioda-ku, Tokyo 102, Japan. No. 1: x + 139 pp. in Japanese, x + 113 pp. in English, 70 color plates, plus text figures. No. 2: xiii + 89 pp. in Japanese, xi + 33 pp. in English, 48 color plates, plus text figures. No ISBN number. Hardcover, 19 × 27 cm. Price 17,500 yen (approx. \$137.00 U.S.). Order from TTS Books, 100-239 Oni-gasawa Uchigoumiya-Machi, Iwaki-shi Fukushima Pre., 973 Japan.

In 1988, Kazuhisa Otsuka authored Volume I of *Butterflies of Borneo* (see review by T. C. Emmel, 1990, *Journal of the Lepidopterists' Society*, 44(2):105–106), which covered 327 species in seven families (Papilionidae, Pieridae, Danaidae, Satyridae, Libytheidae, Nymphalidae, and Riodinidae). Remarkably, the authors have now carried their pledge (almost to the day) to publish “a second volume in two years” that would cover the 600 species of Lycaenidae and HesperIIDae found in Borneo. And a wonderful work it is, much improved over even the highest standards of Volume I.

Because these last two families have special taxonomic problems, Otsuka invited three younger colleagues to help him prepare Volume II. Following the publication of Volume I in 1988, all the authors made four expeditions to Borneo for special coverage of unexplored areas, and they also travelled to the Natural History Museum, London, and other European museums to collect data on Borneo specimens. The extra effort shows to great advantage in this coauthored project.

The color plates in both parts of Volume II are superb, with life-sized reproductions of both lycaenids and hesperiids (including both the upperside and underside of the male and female of each species). The organization and comprehensiveness of the individual species accounts have been much improved in this second volume. For each genus, there is given a key to species and a description of its geographical distribution, number of species, and behavioral habits. Then, in each species account, a code letter and number (which cross-reference the species name to the plate) introduce the species and subspecies name, author, and date of description. A relevant synonymy is given, followed by forewing length measurements of the male and female. Geographical distribution of the species in Borneo is given in detail and distribution outside of Borneo is also covered. Ranges of other subspecies are listed, and food plants recorded both in Borneo and elsewhere are given. A citation for the locality information for each figured specimen concludes the account. No references are given in the HesperIIDae section, but one can refer to Charles A. Bridges' bibliography of literature on butterflies of the world to locate the author and date citations. In the Lycaenidae volume (Part I), a good bibliography of selected references is given with full citations.

There are many surprises in this book, and these help to make it a highly important reference for all students of southeast Asian island butterfly groups. For example, who would have guessed that there are at least 91 species of the spectacular hairstreak genus

Arhopala in Borneo, or at least 22 species of the strange genus *Allotinus* in the subfamily Miletini, or 12 species of *Miletus* itself? A host of *Celastrina* blues, and spectacular long-tailed *Drupadia* hairstreak species, make one want to take the next plane to Borneo to explore and study the endless variety of these groups there!

In addition to providing an excellent guide to identification and some details of the basic biology of these two major families of butterflies in Borneo, the authors include pictures in color and words of the richness of the Bornean habitats that still remain. Yet they warn that during the two short years since the publication of Volume I, forests have continued to be destroyed for the sake of local economic development, especially for the export of forest timber to Japan. As the editor, Kazuhisa Otsuka, aptly says in his Foreword, "The tropical rain forest and its rich life should last forever for the earth as well as for us. The beautiful green world where birds sing, flowers bloom, and nymphs (butterflies) dance, should not be harmed any more beyond the present state. Otherwise, it will eventually lead to an unnatural extinction of human being."

Together with the plates, this fascinating text (published in full in both Japanese and English) provides a rich introduction to the incredible butterfly fauna of Borneo. The excellent text figures, maps, and separate keys for males and females provide the elements of a model work for others to emulate. Any lepidopterist or scientist interested in the butterflies of southeast Asia will want to add both volumes of this work to his or her library. Naturalists or lepidopterists fortunate enough to visit Borneo will want to take these volumes into the field as a guide to the incredible diversity of butterflies in this fascinating part of Malaysia.

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THE COMMON NAMES OF NORTH AMERICAN BUTTERFLIES, edited by Jacqueline Y. Miller (Forward by Paul A. Opler). 1992. Smithsonian Institution Press, Washington, DC. ix + 177 pp. Soft cover, 15 × 23 cm., ISBN 1-56098-122-9, \$14.95.

This book presents a taxonomic list of the North American Butterflies, with the common names that have been used for each. Most common names have the source listed, if the source was an important book on the North American butterflies. Common names are even listed for all subspecies.

The book could prove useful to persons wanting to choose among the various common names that have been applied to a species. Where the book disappoints, however, is its designation of recommended common names in boldface. The foreword by Paul Opler even encourages authors to use the recommended names universally, a noble goal if the recommended names were good appropriate names. Unfortunately, in recommending inappropriate or misleading common names for hundreds of species, this book is a backward step. ICZN rules state that misleading or inappropriate or bad-sounding scientific names cannot be replaced, so we are forced to endure for eternity such blatant errors as *Plebejus lupinus*, a butterfly whose larvae eat *Eriogonum* and never go near *Lupinus* and whose adults never visit *Lupinus* flowers, which can be harvested only by brutish hymenopterans such as bumblebees. The virtue of common names is that they can be corrected, improved, or invented by anyone, so we should not tolerate bad or misleading common names. This book is basically hostile to the idea of common names, because its recommendations are rigidly based on frequency of past usage rather than appropriateness or inappropriateness of the name itself, a procedure surely as heartless as the strict priority mandated by the ICZN; in virtually every case—involving hundreds of names—the book passes up the more appropriate name if the worse name has been used more often. Thus the book recommends the erroneous common name of Lupine Blue for *P. lupinus* (a

name terrifically applicable to *Plebejus icarioides*); Sleepy Orange for *Eurema nicippe*, a butterfly whose flight is both fast and erratic, the antithesis of sleepy; Tawny Crescent for *Phyciodes batessi*, which is not tawny; Southern Cloudy Wing for *Thorybes bathyllus*, a name only appropriate for *Thorybes confusus*; Dark Wood Nymph for *Cercyonis oetus*, one of whose subspecies is the Pale Satyr; Sheep Skipper for *Atrytonopsis ovinia edwardsi*, a name based on the misconception that Navajo sheep occupy the same range as the butterfly (the sheep actually occupy northern, the butterfly southern, Arizona); Dusky Azure for *Celastrina nigra*, whose wings are not azure; Great Purple Hairstreak for *Atlides halesus*, whose wings are not purple; Clouded Sulphur for *Colias philodice*, whose wings are not clouded; the Twin-spot Skipper for *Oligoria maculata*, which has three spots; the Silver-bordered Fritillary for *Boloria selene*, whose silver spots cover the whole wing; Sonora Blue for *Philotes sonorensis*, which is not found in Sonora; Reddish Hairstreak for *Strymon rufofusca*, which is not reddish; Early Hairstreak for *Erora laeta*, which is not early, the second flight being July–August and the first May–June (the book ignores the far better name Turquoise Hairstreak, which is quite appropriate for the blue-green, flecked-with-brown underside of this insect, like a little turquoise jewel); Gray Comma for *Polygonia prognæ*, which is blackish-gray (gray fits only *P. gracilis/zephyrus*); the list goes on and on. Sometimes the book inexplicably passes over a better name that has been used more often in favor of an earlier name used only once (*Myscelia ethusa*, *Lycaena arota*, etc.). Tautonyms are uniformly recommended over more appropriate names, another sign of the book's basic hostility against common names. Common names widely accepted in Europe (*Lycaena phlaeas*, *Boloria napaea*, *Pontia*, *Pieris*, *Euchloe*, etc.) are ignored. Hundreds of common names are misnamed from one small part of a vast range (West Coast Lady, Shasta Blue, etc.). My own 1986 book (*The Butterflies of North America, A Natural History and Field Guide*, Stanford University Press, 583 pp.) corrected the misleading and inappropriate names and improved many others, yet the present book rejects nearly all of the corrections and improvements in favor of bad names oft-repeated. The relative inexperience of the author concerning butterflies prevented her from recognizing many of these bad names and from considering the behavior and habitat of each species in recommending a common name. The book is filled with numerous other errors in citations and names: several of the books listed in the literature cited and cited throughout the text (by L. Miller & P. Opler, etc.) do not exist as of this writing; the Sentinel Arctic is not in Pyle (1981, *The Audubon Society Field Guide to North American Butterflies*, Alfred K. Knopf, New York, 916 pp.) as cited; the name *Neonympha sancticrucis* does not exist; the species *Polygonia silvius* does not exist; the same species is listed twice (as *Thorybes valeriana* and *Cogia mysie*); Scott used "Sulfur" not "Sulphur" for Coliadinae and used Brown Peacock for *Anartia fatima*; Lehman's Checkerspot is listed after the wrong subspecies; Scott did not use Anchisiades Swallowtail or use Streamlined Dusky Brown for "*Pyrrnis*" *funeralis*, etc. Many scientific names used are ten years out of date.

Lepidopterists should ignore the boldface recommendations in this book and use only good appropriate names. The study of butterflies is young compared to the study of birds (because there are fifty times more ornithologists working on half the number of species), so there is no need to rush into mandating particular common names when so many of them are bad. The lesson from this unfortunate book is this: common names SHOULD be appropriate descriptive names for the common person; they should NOT be the most common error.

JAMES A. SCOTT, 60 Estes Street, Lakewood, Colorado 80226.

OBITUARY

WILLIAM DEWITT FIELD (1914-1992)

William Dewitt Field was a curator of entomology at the United States National Museum, Smithsonian Institution, for over 30 years. He published 49 papers on Lepidoptera, primarily butterflies, during the period 1934-77, and one more is in press. His major interest was butterfly literature and nomenclature, as well as jazz music (he kept an extensive collection of LP records at his home in Falls Church, Virginia). Perhaps his best known work was the *Manual of the Butterflies and Skippers of Kansas* (1940), which was based on his Master's Thesis. In the latter part of his career his research included revisionary studies of various butterfly and moth groups and compilations of literature on butterflies.

Bill Field was born in Lawrence, Kansas, on 3 December 1914. He earned his B.A. (1936) and M.A. (1938) at the University of Kansas, and held a Graduate Fellowship there from 1938-40. From September 1936 to September 1938 he also held a curatorship at the Cheyenne Mountain Museum, Colorado Springs, Colorado, and taught courses in biology at Mountain Valley School for Boys in Colorado Springs. He was hired in September 1940 as an Assistant Entomologist by the Division of Insect Identification, U.S. Department of Agriculture.

Bill joined the U.S. Army in 1943 and served with the Malaria Survey Unit until 1946, at which time he rejoined the Division of Insect Identification as an entomologist. The following year (1947) he transferred to the Smithsonian Institution's Division of Insects as a curator of entomology, a position that he held until his retirement on 30 August 1980. Probably his best friend was José Herrera, a lepidopterist from Chile with whom Bill conducted research on Andean-Patagonian pierids. Gerardo Lamas held a postdoctoral fellowship with Bill (1976-77), at which time they began work (with Richard G. Robbins) on the *Bibliography of Neotropical Butterflies*.

William Field's post-employment years were dedicated to gardening, but poor health interfered with this avocation and eventually led to his death on 20 February 1992. Bill is survived by his second wife, Madeleine, and four children.

LIST OF PUBLICATIONS BY WILLIAM FIELD

1934

1. On the naming of "transition forms" in Lepidoptera with notes on certain forms captured near Lawrence, Kansas. *Canad. Entomol.* 66:253-257.

1936

2. Three new butterfly races. *Entomol. News* 47:121-124.
3. New North American Rhopalocera. *Pomona Coll. J. Entomol. Zool.* 28:18-26.

1937

4. A new seasonal form of *Coenonympha ampelos* Edwards. *Canad. Entomol.* 69:249-250.

1938

5. A new butterfly record for the United States. *Entomol. News* 49:28.
6. Variation in *Habrodais grunus* (Boisduval). *Bull. Southern California Acad. Sci.* 37: 23-29.
7. A new race of *Lycaena mariposa* (Reakirt). *Pan-Pacif. Entomol.* 14:142-143.
8. New forms and subspecies of North American Libytheidae and Lycaenidae. *J. Kansas Entomol. Soc.* 11:124-133.

1939

9. A new species of *Plebejus* Kluk from Idaho. *J. Kansas Entomol. Soc.* 12:135-136.

1940

10. Distribution notes on *Amblyscirtes nysa* Edwards. *J. Kansas Entomol. Soc.* 13:7.
11. New records of butterflies for Kansas. *J. Kansas Entomol. Soc.* 13:28-29.
12. Some unusual butterfly records for Kansas. *J. Kansas Entomol. Soc.* 13:50.
13. Distributional notes on *Copaeodes aurantiaca* (Hewitson). *J. Kansas Entomol. Soc.* 13:50.
14. A distribution note on *Grais stigmaticus* (Mabille). *J. Kansas Entomol. Soc.* 13:57.
15. A new skipper record for the United States. *J. Kansas Entomol. Soc.* 13:57.
16. A manual of the butterflies and skippers of Kansas. *Bull. Dept. Entomol. Univ. Kansas*, number 12 [*Bull. Univ. Kansas* 39(10):1-327].
17. A distributional note on *Achalarus lyciades* (Geyer). *J. Kansas Entomol. Soc.* 13:114.
18. A distributional note on *Heterochroa bredowii* (Geyer). *J. Kansas Entomol. Soc.* 13: 123.
19. A note on *Argynnis cybele krautwurmi* Holland. *J. Kansas Entomol. Soc.* 13:229.
20. *Calycopsis beon* (Cramer), a new butterfly record for the United States. *Bull. Brooklyn Entomol. Soc.* 35:134-135.
21. Distributional notes and comments upon a collection of Mexican Lepidoptera. *Bull. Univ. Kansas* 41:339-354.

1941

22. Additional notes on *Calycopsis cecrops* (Fabricius) and *Calycopsis beon* (Cramer). *J. Kansas Entomol. Soc.* 14:66-69.

23. Notes on *Erora laeta* (Edwards) and *Erora quaderna* (Hewitson). Ann. Entomol. Soc. Am. 34:303-316.

1942

24. Racial variation in *Hemiargus isola* (Reakirt). J. Kansas Entomol. Soc. 15:36.
25. Racial variation in *Strymon columella* (Fabricius). J. Kansas Entomol. Soc. 16:153.

1948

26. The correct name for the North American butterfly variously called *Nymphidia*, *Calephelis* or *Lephelisca*. Proc. Entomol. Soc. Washington 50:207-213.

1950

27. Moths of the genus *Cincia* and three new and closely related genera. Proc. U.S. Natl. Mus. 100:311-326.
28. The International Commission on Zoological Nomenclature and the correct name for the North American monarch butterfly. Proc. Entomol. Soc. Washington 52:234-236.

1951

29. On a recent proposal to correct an error committed by the International Commission on Zoological Nomenclature at the Paris 1948 Meeting. Science 113:68-70. With J. F. Gates Clarke and John G. Franclemont as junior authors.
30. Moths of the genus *Paramulona* Hampson. Proc. U.S. Natl. Mus. 101:489-496.
31. On the proposed suppression of the trivial name "ajax" Linnaeus, 1758. Bull. Zool. Nomen. 6:105-106.
32. A revision of *Eurema* Hübner subgenus *Teriocolias* Rober. Acta Zool. Lilloana 9:359-374.

1952

33. Moths of the genus *Mulona* Walker and *Lomuna*, a new and closely related genus. Proc. U.S. Natl. Mus. 102:221-230.
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1958

35. A redefinition of the butterfly genera *Tatochila*, *Phulia*, *Piercolias*, and *Baltia*, with descriptions of related genera and subgenera. Proc. U.S. Natl. Mus. 108:103-131.

1959

36. A revision of the butterfly genera *Theochila* and *Tatochila*: Lepidoptera, Pieridae. Proc. U.S. Natl. Mus. 108:467-514. With Jose Herrera as senior author.

1964

37. Moths of the genus *Rhabdatomis* (Arctiidae: Lithosiinae). Proc. U.S. Natl. Mus. 115: 46-60.

1966

38. Preliminary revision of the butterflies of the genus *Calycopis* Scudder (Lycaenidae: Theclinae). Proc. U.S. Natl. Mus. 119:1-48.

1967

39. Butterflies of the new genus *Calystryma* (Lycaenidae: Theclinae, Strymonini). Proc. U.S. Natl. Mus. 123:1-31.

1970

40. List of the butterflies of Kansas, including native and visitant species. Mid-Continent Lepid. Ser. 13:1-16. [A reprint of paper number 16 of this list, pages 273-288.]
41. *Papilio hyllus* Cramer, 1776, vs. *Polyommatus thoe* Guérin-Meneville, 1831, and the "50-year rule." J. New York Entomol. Soc. 78:175-184. With F. Martin Brown as senior author.

1971

42. Butterflies of the genus *Vanessa* and of the resurrected genera *Bassaris* and *Cynthia* (Lepidoptera: Nymphalidae). Smithsonian Contrib. Zool. 84:1-104.

1972

43. Introduction (page i) to "Report on a Collection of Butterflies made mostly at Ft. Chimo, Ungava, Hudson Strait, by L. M. Turner in July, August and September, 1883-4," by W. H. Edwards. Mid-Continent Lepid. Ser. 2(32).
44. Introduction (pages i, ii) to "An Index to the Described Life Histories, Early Stages and Hosts of the Macrolepidoptera of the Continental United States and Canada," by Harrison Morton Tietz. Allyn Mus. Entomol. 1041 pages. With J. F. Gates Clarke.

1973

45. African butterflies: Three book reviews. Bull. Entomol. Soc. Am. 19:223-224.

1974

46. Four book reviews: Butterflies of the Australian region, by Bernard D'Abrera, 1971; Australian butterflies, by Charles McCubbin, 1971; Butterflies of Australia, by Ian F. B. Common and Douglas F. Waterhouse, 1972; Jamaica and its butterflies, by F. Martin Brown and Bernard Heineman, 1972. Proc. Entomol. Soc. Washington 75: 486-488.
47. A bibliography of the catalogs, lists, faunal and other papers on the butterflies of North America north of Mexico arranged by state and province (Lepidoptera: Rhopalocera). Smithsonian Contrib. Zool. 157:1-104. With Cyril F. Dos Passos and John H. Masters as junior authors.

1975

48. The ctenuchid moths of the genera *Ceramidia* Butler, *Ceramidiodes* Hampson and the *caca* group of the genus *Antichloris* Hübner. Smithsonian Contrib. Zool. 198: 1-45.

1977

49. The pierid butterflies of the genera *Hyposchila* Ureta, *Phulia* Herrich-Schaffer, *Infraphulia* Field, *Pierphulia* Field, and *Piercolias* Staudinger. Smithsonian Contrib. Zool. 232:1-64. With José Herrera as junior author.

1993

50. A bibliography of the Neotropical butterflies. In Heppner, J. B. (ed.), Atlas of Neotropical Lepidoptera. *In press*. With Gerardo Lamas and Richard Robbins as senior authors.

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——— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. *Adv. Genet.* 10:165–216.

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Cover illustration: The monarch butterfly (*Danaus plexippus* L.) is well known for its arduous, long distance seasonal migration. It is thought to be the unpalatable model for the Batesian mimic viceroy butterfly (*Limenitis archippus* Cramer). The monarch is found throughout the United States. Original drawing by Kojiro Shiraiwa, 343 East 15th Street, Eugene, Oregon 97401-4209.

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COMMENTS ON THE GENUS *POLITES*, WITH THE DESCRIPTION OF A NEW SPECIES OF THE *THEMISTOCLES* GROUP FROM MEXICO (HESPERIIDAE: HESPERIINAE)

C. DON MACNEILL

Department of Entomology, California Academy of Sciences, Golden Gate Park,
San Francisco, California 94118-4599

ABSTRACT. The *themistocles* group is distinguished from three other elements of the genus *Polites* Scudder on the basis of the stigma of the male and the genitalia of both sexes. The male and female genitalia of the *themistocles* group are comparatively illustrated (the female for the first time). A new, astigmal species, *Polites nora*, is described and illustrated from Sonora, Mexico.

Additional key words: genitalia (male and female), *Polites baracoa*, *Yvretta*, *Hylephila*, *Wallengrenia*.

Polites Scudder is a principally North American genus of at least a dozen species, most of which occur within the United States. Skinner and Williams (1924) figured the male genitalia of our species of *Polites*, and these figures were reproduced by Lindsey, Bell and Williams in 1931 under the genus *Talides* Hübner. These remained the only comparative genitalic illustrations of the genus until Evans' (1955) caricatures appeared. Because the male genitalia of the closely related species within each of several assemblages are very similar, Evans' inaccurate and incomplete figures are not useful. The Skinner and Williams illustrations, while relatively accurate, suffer distortion and orientation differences owing to slide preparation, so that they mask similarities and suggest greater differences than exist.

Male genitalic similarities suggest that the nearest relatives of *Polites* are the genera *Yvretta* Hemming, *Hylephila* Billberg, and *Wallengrenia* Berg. *Polites* is not closely related to *Hesperia* Fabricius as repeatedly maintained by Scott (1992:1, 126, 167, 168). Based on the male and female genitalia and features of the male stigma, four distinct elements can be identified within *Polites*: *Polites baracoa* (Lucas), the

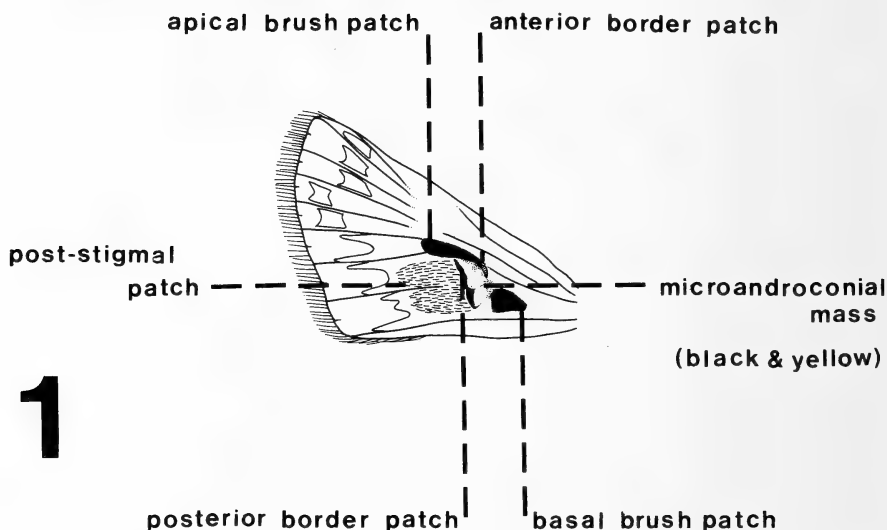
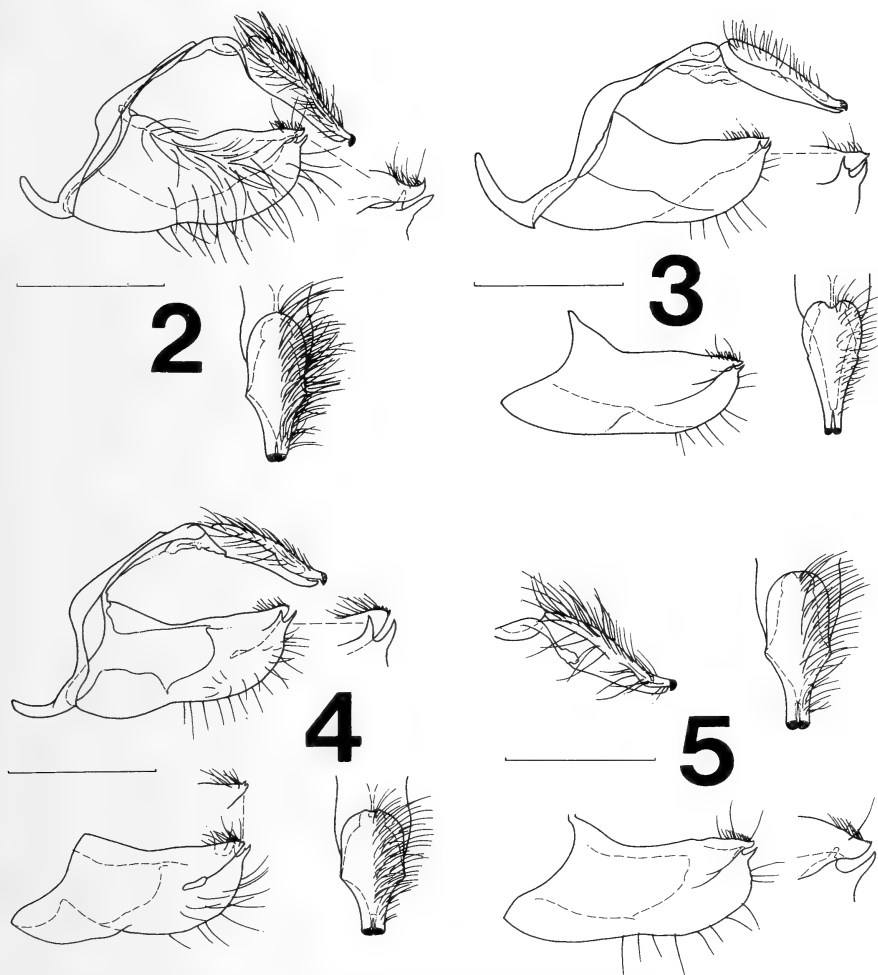


FIG. 1. Diagram of left forewing of *Polites draco* male illustrating stigma structures.

vibex group, the *origenes* group, and the *themistocles* group. *Polites baracoa* is peculiar. Although it retains the general stigmal and genitalic plan of *Polites*, it departs in most details from other groups. In particular, males seem to have lost, at the dorsocaudal tip of the uncus, the pair of shiny patches (pectines) that are minutely striated longitudinally. These terminal uncal pectines are characteristic of *Polites* and all related genera.

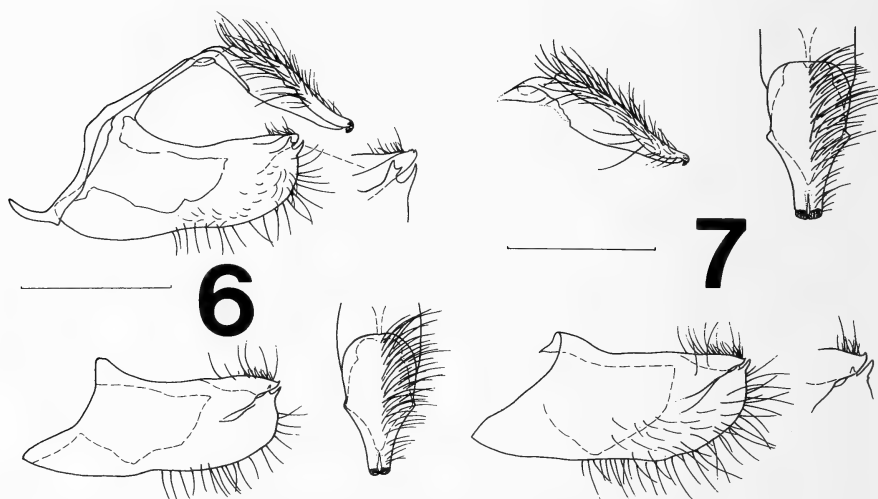
The five species *P. themistocles* (Latreille), *P. peckius* (Kirby), *P. mardon* (Edwards), *P. draco* (Edwards), and *P. sabuleti* (Boisduval) constitute the *themistocles* group. All have such remarkably similar male genitalia that individual variability sometimes equals the apparent specific differences. Thus Evans (1955) viewed the three "western" species as conspecific. Although *P. mardon*, *P. draco*, and *P. sabuleti* are apparently allopatric or allochronic, they approach one another very closely in many areas and show no evidence of introgression. Scott (1986:443) claimed intermediates between *sabuleti* and *draco* but later (1992:127) withdrew the statement. The morphology and biology of these three entities seem sufficiently distinct (Comstock 1929:25, Dethier 1943:128, Newcomer 1966:243, Emmel and Emmel 1973:82, MacNeill 1975:483, Stanford 1981:118, Scott 1992:125) to consider them species.

Polites mardon retains its integrity (but with apparent population differences) from Washington to California, with its stubby wings, vague (often fuzzy) markings, reduced stigmal elements, distinctive male and



FIGS. 2-5. Uncus, tegumen (left lateral and dorsal aspects and valvae (lateral aspects) of male genitalia of two species of *Polites*. Bar equals 1 mm. **2**, *Polites sabuleti sabuleti*, Sherman Isl., Sacramento Co., California, 4 October 1969, D. F. Shillingburg (genitalic dissection no. 6021-CDM); **3**, *Polites sabuleti sabuleti*, Asilomar, Monterey Co., California, 26 September 1959, C. W. O'Brien (genitalic dissection no. 3988-J. Herrera); **4**, *Polites sabuleti margaretae*, paratype, S.E. shore of La Paz harbor, B.C.S., MEXICO, 6 December 1961, Cary-Carnegie Expedition 1961 (genitalic dissection no. 6014-CDM); **5**, *Polites draco*, nr. Antero Jct., Park Co., Colorado, 1 June 1974, R. E. Stanford (genitalic dissection no. 6023-CDM).

female genitalia (Figs. 8, 17, 24), oviposition without adhesive (MacNeill unpubl. data), size and color of ova, and color pattern and chaetotaxy of larvae and pupae (Newcomer 1966, MacNeill unpubl. data). *Polites draco* also is possibly polytypic. Scott (1986:443) asserted that it is

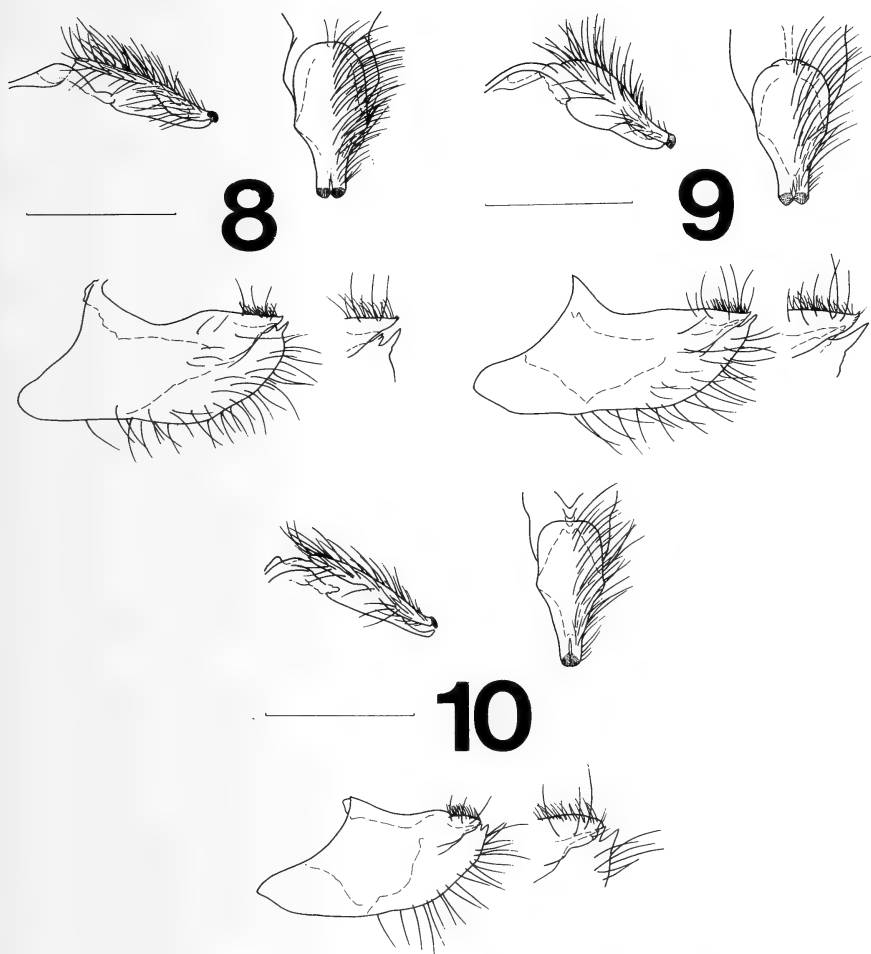


FIGS. 6, 7. Uncus, tegumen (left lateral and dorsal aspects and valvae (lateral aspects) of the male genitalia of *Polites norae*. Bar equals 1 mm, 6, Paratype, Bacochibampo Bay, vic. Guaymas, Sonora, MEXICO, 22 April 1988, C. D. MacNeill & N. MacNeill-Manss (genitalic dissection no. 6013-CDM); 7, Paratype, same data as above (except genitalic dissection no. 6012-CDM).

“probably an altitudinal ssp. of *sabuleti*” but later recanted (Scott 1992: 127) that contention. From the Yukon south to New Mexico, Arizona, and possibly southern Nevada *Polites draco* retains its distinctive markings (though these vary somewhat with altitude [Brown 1962] and latitude), color and form of the male stigma (but in Wyoming the stigma color varies), characteristic male and female genitalia (Figs. 1, 5, 14, 27), size and color of ova and first instar larvae (Scott 1992, MacNeill unpubl. data), and setal characteristics of the latter (MacNeill unpubl. data).

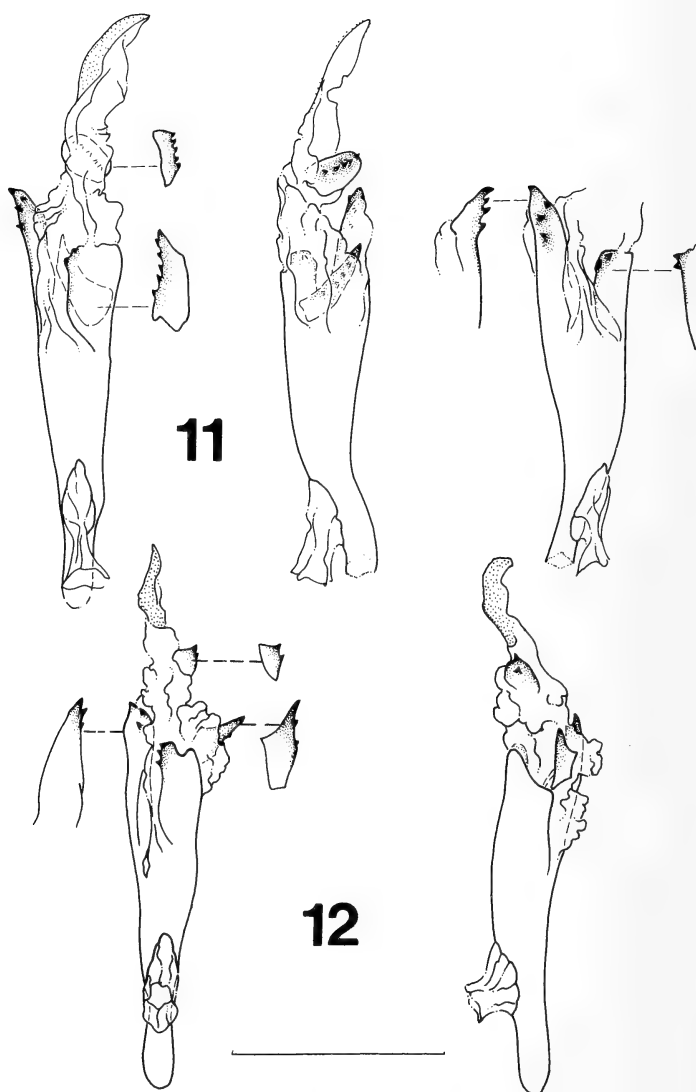
Polites sabuleti (Figs. 2–4, 11–13, 20, 21, 23, 25) is not well understood at present. It is polytypic through its wide distribution from British Columbia to the southern tip of Baja California Sur and eastward across Idaho into Colorado and New Mexico, with an ecological and altitudinal range from the coastal strand and salt marsh at sea level to alpine fell fields at over 4000 m in California. It was reviewed thoroughly for Nevada by Austin (1987, 1988). I am convinced that more than one species goes under this name—a possibility mentioned by Shapiro (1975: 37)—but a much better understanding of the many named and unnamed populations ascribed to *sabuleti* requires further study.

Polites peckius (Figs. 9, 18, 28) without adhesive (Scudder 1889: 1687, Scott 1992:124, 129, 130) and *P. themistocles* (Figs. 10, 19, 29) with adhesive during oviposition are principally eastern, though both



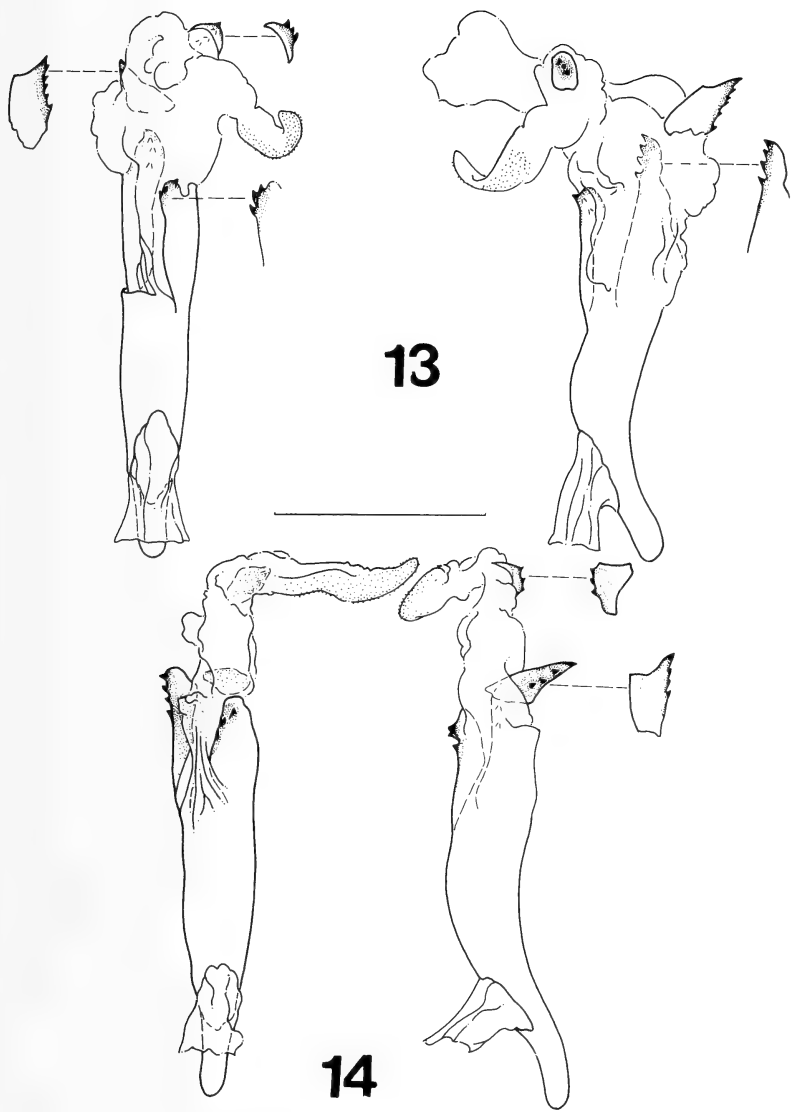
FIGS. 8–10. Uncus, tegumen (left lateral and dorsal aspects) and valvae (lateral aspects) of the male genitalia of three species of *Polites*. Bar equals 1 mm. **8**, *Polites mardon*, Signal Peak, Yakima Co., Washington, 22 June 1965, E. J. Newcomer (genitalic dissection no. 6009-CDM); **9**, *Polites peckius*, Trail, British Columbia, CANADA, 1952, A. C. Jenkins (genitalic dissection no. 6024-CDM); **10**, *Polites themistocles*, nr. Dead Horse Summit, 5 mi S. E. Bartle, 1280 m, Siskiyou Co., California, 3 July 1963, C. D. MacNeill (genitalic dissection no. 6027-CDM).

range through the Rocky Mountains and beyond into several Pacific Coast states or provinces. Although each also may be more than one entity, they maintain their morphological and biological distinctness (Scudder 1889, Dethier 1938, 1939, 1942, Shapiro 1974, Stanford 1981, MacNeill 1975, Scott 1992) everywhere they approach or interdigitate with other species of the group.



FIGS. 11, 12. Penis (vesica everted) of male genitalia of *Polites sabuleti sabuleti*. Bar equals 1 mm. **11**, Same data as Fig. 2, dorsal, left lateral and right dorso-lateral aspects (tip of coecum penis broken); **12**, Same data as Fig. 3, dorsal and left lateral aspects.

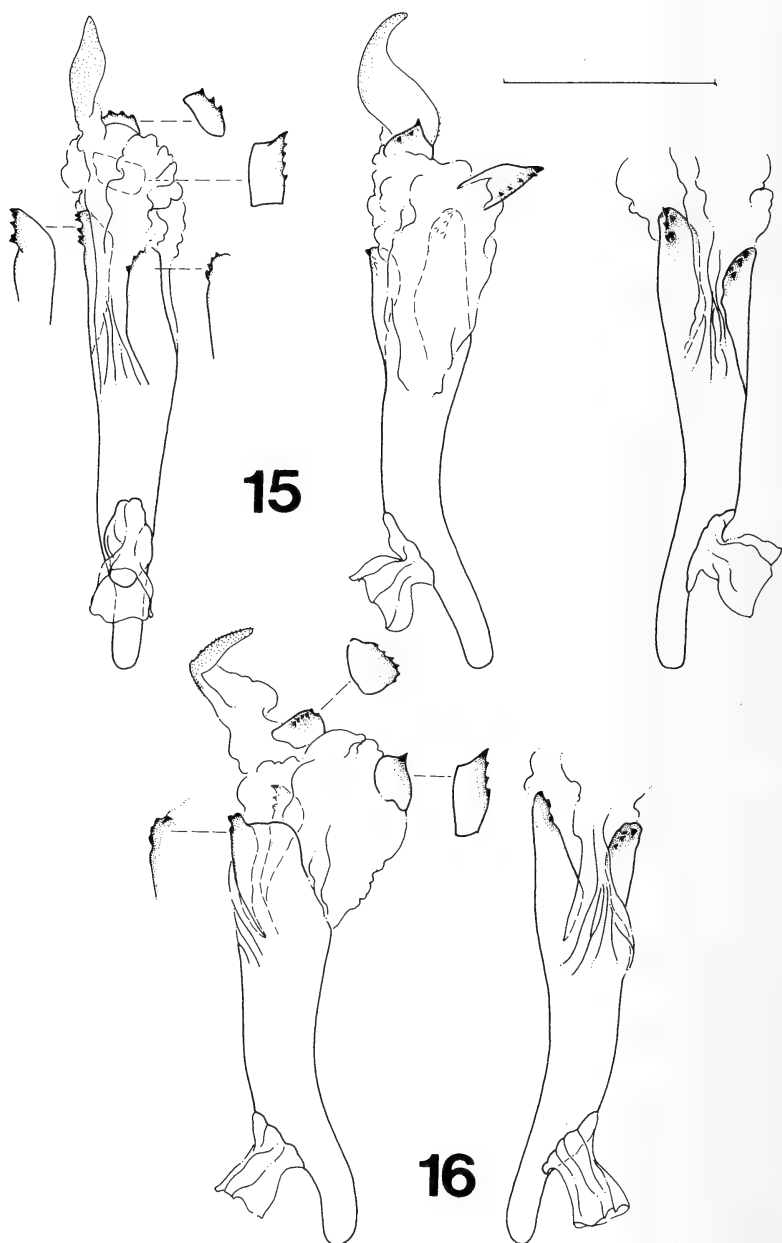
The purpose of this paper is twofold: to provide a brief diagnosis and comparative illustrations of male and female genitalia for the *themistocles* group of *Polites* and to shift our perspective on *sabuleti* (s.l.) by introducing a remarkable new species of the *themistocles* group from Mexico.



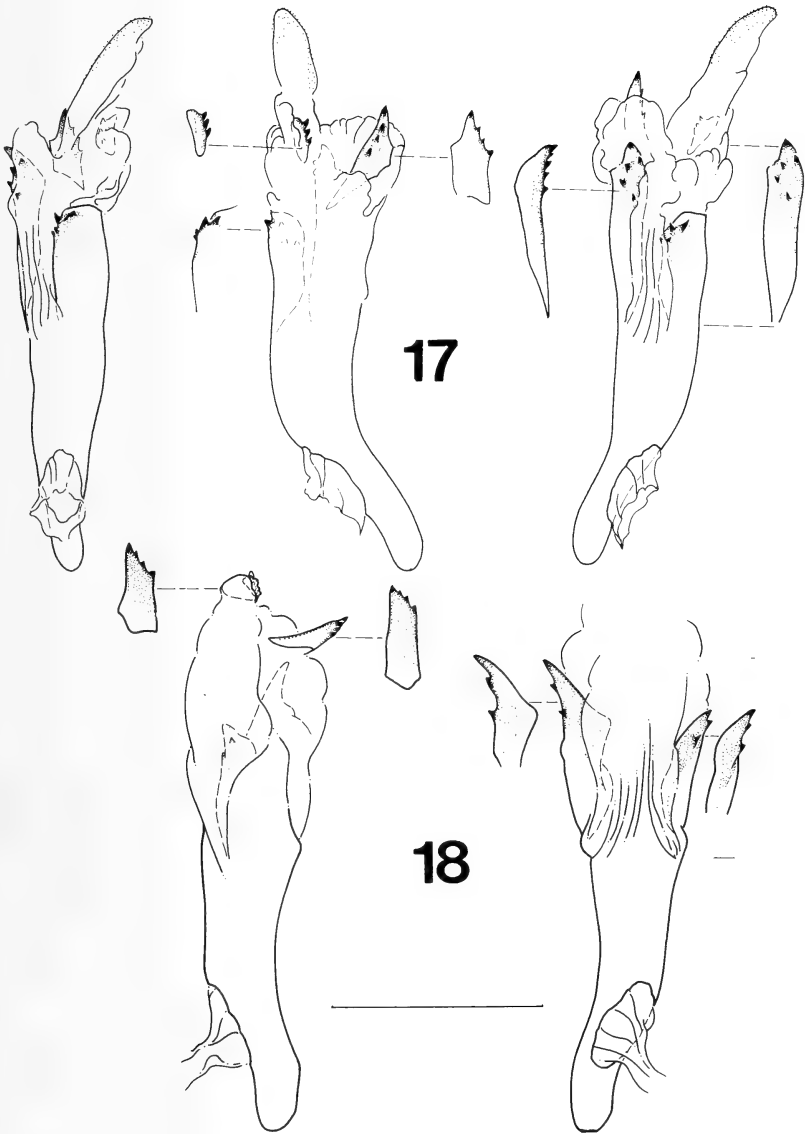
FIGS. 13, 14. Penis (vesica everted) of male genitalia of two species of *Polites*, dorsal and left lateral aspects. Bar equals 1 mm. **13**, *Polites sabuleti margaretae*, same data as Fig. 4; **14**, *Polites draco*, same data as Fig. 5.

DIAGNOSIS OF THE *THEMISTOCLES* GROUP OF *POLITES*

The following features of the male stigma and of the genitalia will distinguish the *themistocles* group of species from the remainder of the genus *Polites*. Terminology for the stigma is a modification of that in MacNeill (1964:49); terminology for the genitalia follows Klots (1970).



FIGS. 15, 16. Penis (vesica everted) of male genitalia of *Polites norae*. Bar equals 1 mm. **15**, Same data as Fig. 6, dorsal, left lateral and right dorso-lateral aspects; **16**, Same data as Fig. 7, left lateral and right dorso-lateral aspects.



FIGS. 17, 18. Penis of male genitalia of two *Polites* species. Bar equals 1 mm. 17, *Polites mardon*, same data as Fig. 8, dorsal, left lateral and right dorso-lateral aspects (vesica everted); 18, *Polites peckius*, same data as for Fig. 9, left lateral and right dorso-lateral aspects (vesica partially everted).

Stigma (if present) (Fig. 1): Apical brush patch conspicuous, broad and long, exceeding apical tip of microandroconial mass by half its length; scales very fine, hair-like, dense and erectile. Basal brush patch large, distinctly offset basad, usually almost separated from basal portion of microandroconial mass, scales hair-like, erectile. Anterior border

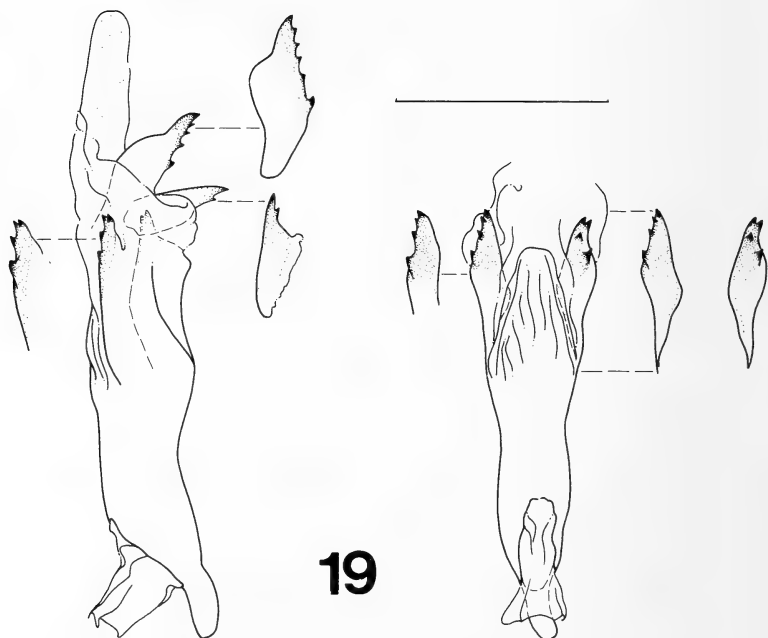


FIG. 19. Penis (vesica everted) of male genitalia of *Polites themistocles*, same data as Fig. 10, left lateral and dorsal aspects. Bar equals 1 mm.

patch conspicuous to obsolete. Posterior border patch conspicuous, broad to slender. Microandroconial mass broad and short, total length subequal to length of apical brush patch, scales very minute, linked sausage-like, often placed in two longitudinal zones of different colors and different scale structure and link lengths. Post-stigmal patch massive to inconspicuous.

Male genitalia (Figs. 2–19): Penis stout; aedeagus abruptly thickened at ductus ejaculatorius to about twice width of coecum penis (phallobase?) in lateral view, not caudally prolonged into a mid-ventral spur; coecum penis short, in lateral view not, or scarcely, longer than mid-aedeagus width; separated lateral, elongate rostellae (titillators of Burns 1987) more or less dorsad, the left usually more dorsal than the right and usually much shorter, not united ventrally; vesica with three cornuti, one a minutely scobinate area along one side of an elongate, finger-like pouch, the other two usually dissimilar sclerotized, thorn-like or multidentate, coned or tented structures that are not themselves enveloped on one side. Uncus only slightly upturned at tip, terminal uncal pectines broad and conspicuous; gnathos not or scarcely exceeding caudal tip. Valva with distal tip of valvula usually dorsally bidentate or weakly tridentate, in caudal view only slightly bent inward (not conspicuously folded) under the flanged caudal tip of the cucullus (but *P. themistocles* tends to have the most strongly inward-bent portion weakly multidentate).

Female genitalia (Figs. 20–29): Ductus bursae more or less well sclerotized, dorsally with a conspicuous longitudinal fold in the ductus roof ending proximally just short of the ductus seminalis, ventrally with a proximal pouch, often less sclerotized. Lamella postvaginalis mostly membranous, only weakly sclerotized as a pair of well separated, vague, curved, longitudinal patches, not sclerotically joined with apophyses anteriores, distally without an isolated, median, sclerotized, finger-like nipple projecting ventro-caudad.

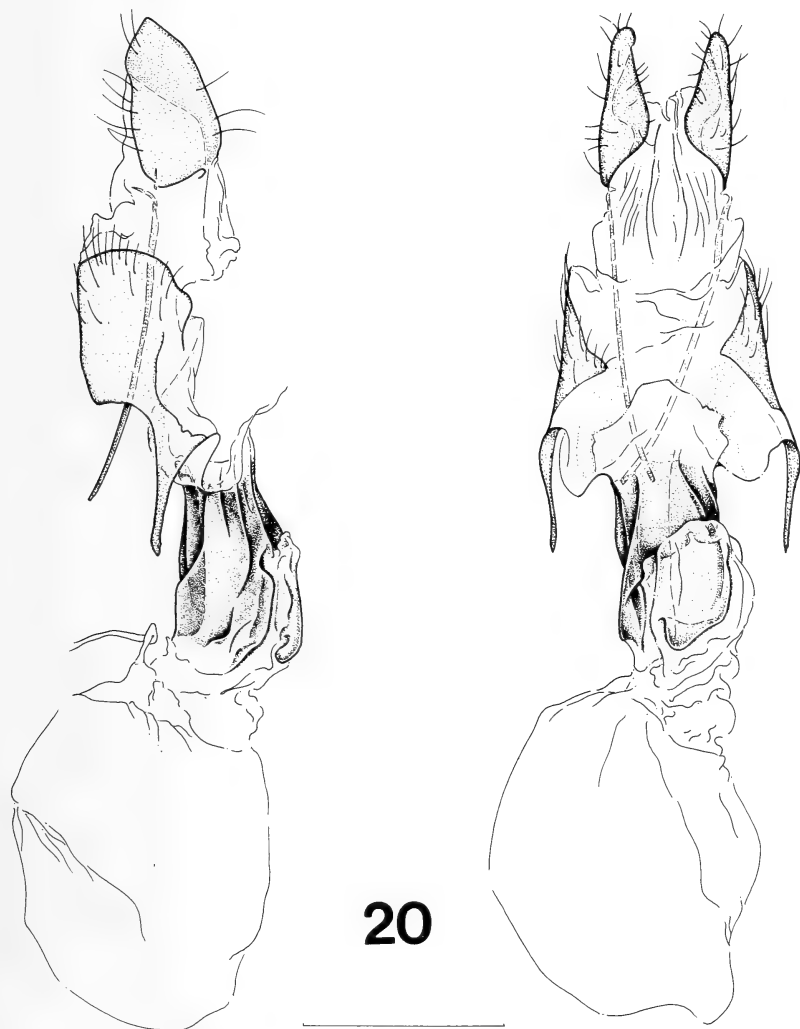


FIG. 20. Female genitalia of *Polites sabuleti sabuleti*, left lateral and ventral aspects, Morro Bay, San Luis Obispo Co., California, 21 October 1979. D. F. Shillingburg (genitalic dissection no. 6049-CDM). Bar equals 1 mm.

Aside from the general color pattern, which is fairly reliable, species within the *themistocles* group of *Polites* may be distinguished by means of the following characters: wing shape, and color and development of different parts of the male stigma. The differences in the male genitalia include the shape of the uncus in dorsal view, the width and development of the "chin" of the valvae, the shape and stockiness of the



FIG. 21. Female genitalia of *Polites sabuleti margaretae*, paratype, left lateral and ventral aspects, S.E. shore of La Paz harbor, B.C.S., MEXICO, 10 November 1961, Cary-Carnegie Expedition 1961 (genitalia dissection no. 6036-CDM).

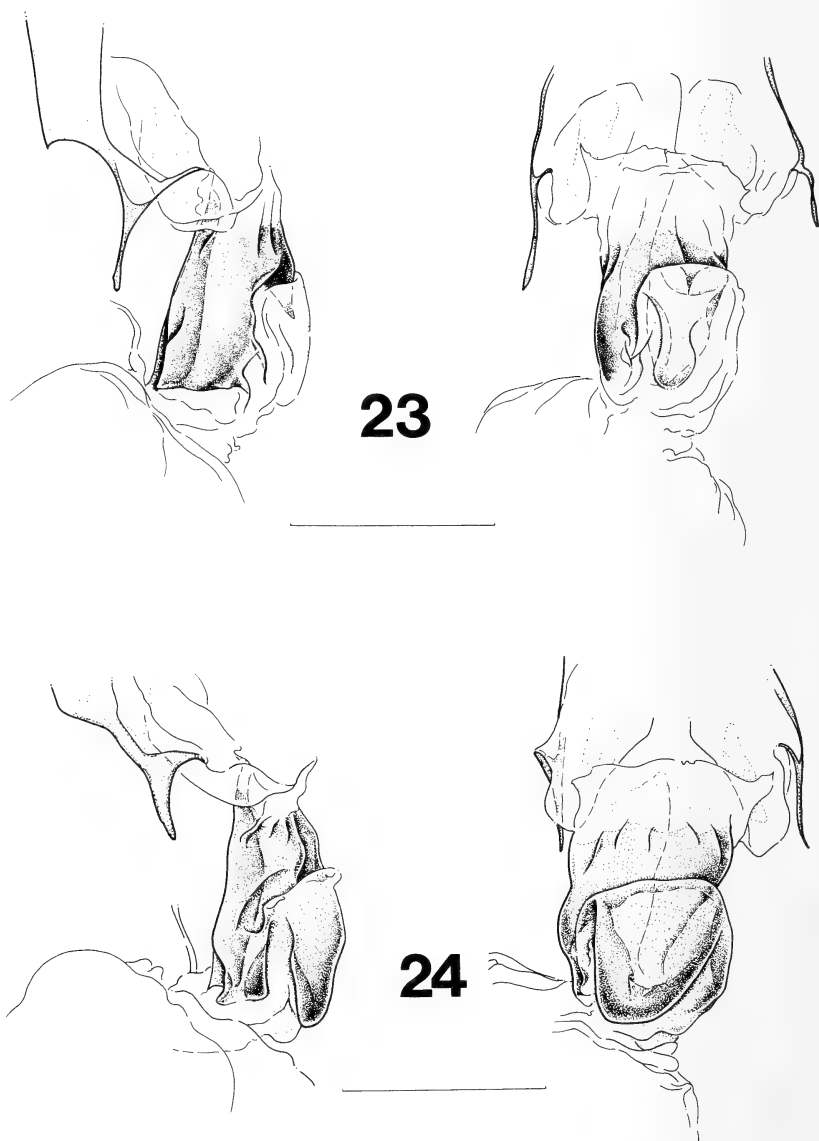
penis, the length and teeth of the rostella, and particularly, the shape and dentition of the cornuti. Female genitalia are useful for discriminating species of the group, especially the wrinkling and sclerotization of the ductus bursae, the development of the ventral pouch, and the



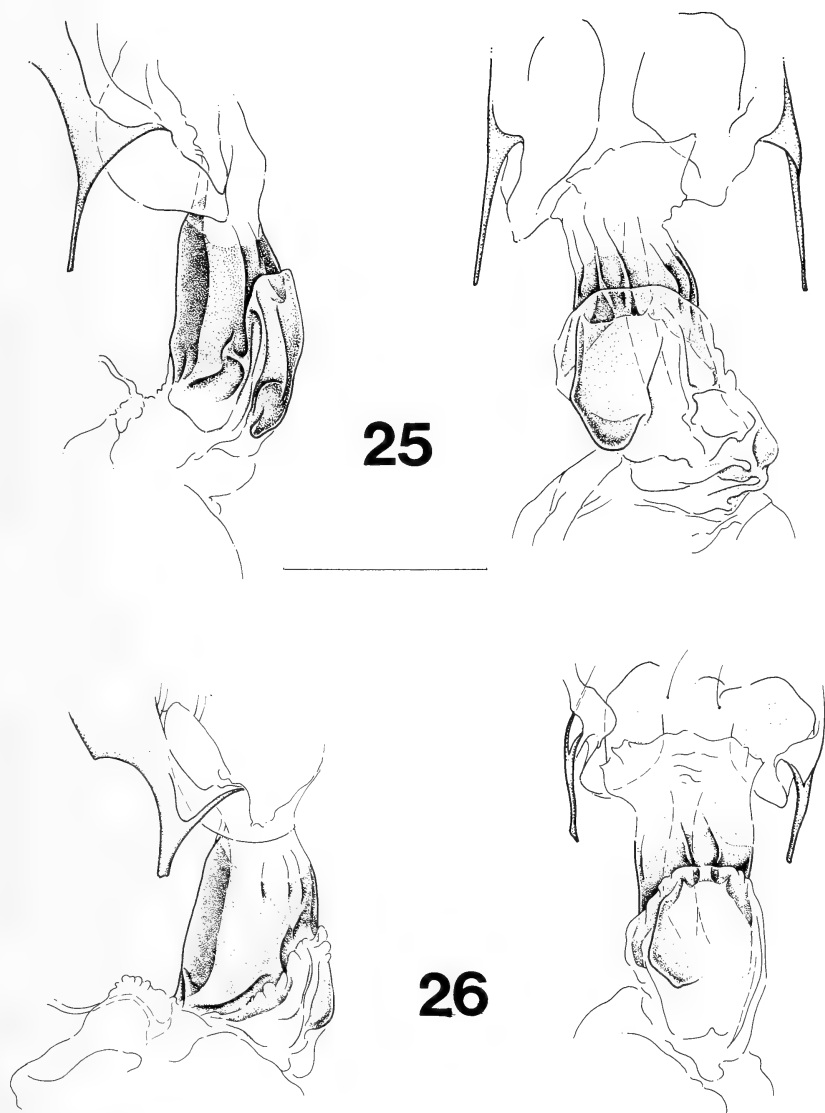
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FIG. 22. Female genitalia of *Polites norae*, paratype, left lateral and ventral aspects. Bacoichibampo Bay, vic. Guaymas, Sonora, MEXICO, 20 April 1988, C. D. MacNeill & N. MacNeill-Manss (genitalic dissection no. 6044-CDM). Bar equals 1 mm.

width and course of the dorsal fold of the ductus. The manner of oviposition, the size and color of the ova, the chaetotaxy of the first instar larvae, and other larval and pupal characteristics also will serve to separate species within this group.



FIGS. 23, 24. Ductus bursae and portions of the corpus bursae and sterigma of the female genitalia of two species of *Polites*, left lateral and ventral aspects. Bar equals 1 mm. **23**, *Polites sabuleti sabuleti*, same data as Fig. 20 (genitalia dissection no. 5048-CDM); **24**, *Polites mardon*, Signal Peak, Yakima Co., Washington, 2 July 1965, E. J. Newcomer (genitalia dissection no. 6038-CDM).



FIGS. 25, 26. Ductus bursae and portions of the corpus bursae and sterigma of the female genitalia of two species of *Polites*, left lateral and ventral aspects. Bar equals 1 mm. **25**, *Polites sabuleti margaretae*, paratype, same data as Fig. 21 but date is 6 December 1961 (genitalia dissection no. 6045-CDM); **26**, *Polites norae*, paratype, same data as Fig. 22 but date is 21 April 1988 (genitalia dissection no. 6035-CDM).

DESCRIPTION OF A NEW SPECIES OF *POLITES*

In my review of the HesperIIDae of Baja California (MacNeill 1962), I noted the resemblance of a single female specimen of *P. sabuleti* from Santa Maria Bay to an undescribed species from the Mexican mainland nearby. The Baja population later was described from maritime grassland as *P. sabuleti margaretae* Miller and MacNeill (1969). The lone male of the new mainland species (from Guaymas, Sonora) remained unique until recently when more material, including two females, became available.

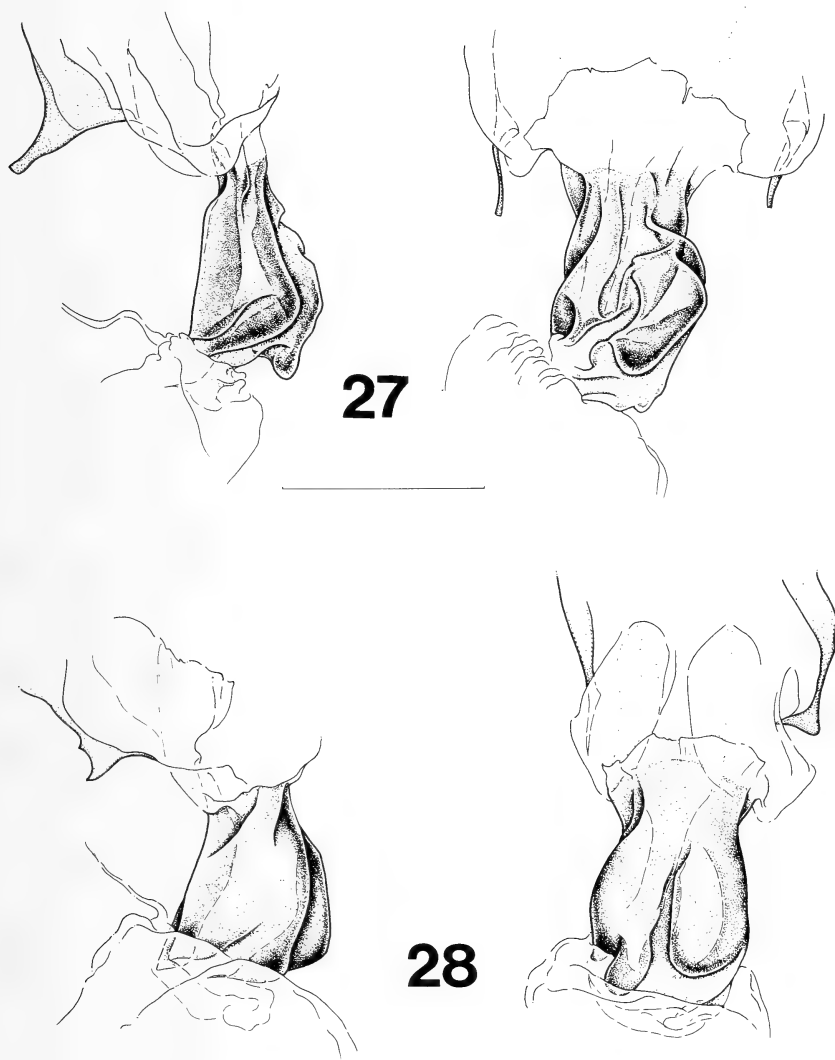
This new species is distinct from all other *Polites* in that males completely lack a stigma. If this and similar structures (costal fold, leg, abdomen or wing brushes, etc.) are pheromonal in function (Muller 1878, Scudder 1889, Barth 1952, 1955) and are important to specific recognition and courtship (MacNeill 1964, Burnes 1964, Scott 1973), then their complete absence in closely related populations implies isolation at the courtship stage. Courtship may even fail owing to communication barriers resulting from slightly differing stigmal structures between populations—different chemical dialects, so to speak. In any case, the structural and biological differences among populations of *P. sabuleti* (s.l.) (Shapiro 1975, MacNeill unpubl. data) require more careful scrutiny in light of the close similarity of the following new species to *P. sabuleti margaretae*.

***Polites norae* MacNeill, new species**

(Figs. 6, 7, 15, 16, 22, 26, 30–33)

Male. Head: Antennal shaft checkered fulvous above, ventrally buffy and laterally black. Club black below apiculus, broadly buff ventrally, and narrowly fulvous on dorsal side of pale brown nudum. Palpal vestiture scaly, not prominently hairy, buff becoming yellow-tinted dorsad, third segment protruding clear of vestiture, black with a few buff scales laterally.

Thorax: Pectus buffy white. Femur outwardly mostly black with buffy scales, inwardly mostly buff, tibia and tarsus buffy. Dorsally black clothed with golden scales. **Wing:** Upper surface. Forewing broadly fulvous from the black-edged costa to space 1a with crisply dentate brown border. Stigma entirely absent. Two discal, oval, brown spots outwardly well defined in spaces 1b and 2, the former tending to extend narrowly and vaguely to base, space 1a with a vague, brown suffusion. Postdiscal elongate, brown spots at end of cell in spaces 4 and 5 and separated by fulvous along vein 5, subapical and subterminal fulvous spots connected by fulvous broadly along vein 6 (which itself is narrowly black). Fulvous of base and disc more reddish orange than the colder fulvous of the subapical and subterminal spots and the spots in spaces 1b to 3. Hindwing brown border distinct and broad, cut deeply along fulvous veins 1b to 6, posterior arm of fulvous macular band narrow and defined inwardly by suggestion of brown spots discally in spaces 2 and 3, as well as in spaces 1c, 5 and 6 and partially in 4, leaving a narrow, fulvous ray conspicuous from near base through lower half of cell to vertex of macular band on spaces 4 and 5. Lower surface. Forewing as above but reddish orange of costa, cell and disc contrasting more with pale subapical, subterminal, and postdiscal spots in spaces 1b, 2 and 3, all of which are extended along veins toward the chocolate brown border which is overscaled with orange. Small, dark brown, oval spot in space 2 separated by yellow vein 2 from



FIGS. 27, 28. Ductus bursae and portions of the corpus bursae and sterigma of the female genitalia of two species of *Polites*, left lateral and ventral aspects. Bar equals 1 mm; **27**, *Polites draco*, Hwy. 91 N.E. Leadville, Lake Co., Colorado, 11 July 1976, R. E. Stanford (genitalia dissection no. 6041-CDM); **28**, *Polites peckius*, Dodgeville, Iowa Co., Wisconsin, 4 July 1950, W. E. Seiker (genitalia dissection no. 6053-CDM).

larger brown spot extending proximally to base in space 1b, the distal edge apically bevelled to a point under outer edge of spot in space 2. Hindwing chocolate brown with contrasting yellow veins and yellow macular band as in *P. sabuleti margaretae*, but the angle of the macular band chevron is wider and the posterior arm more closely parallels the wing margin, the spots of the posterior arm tend to be offset of unequal size so the

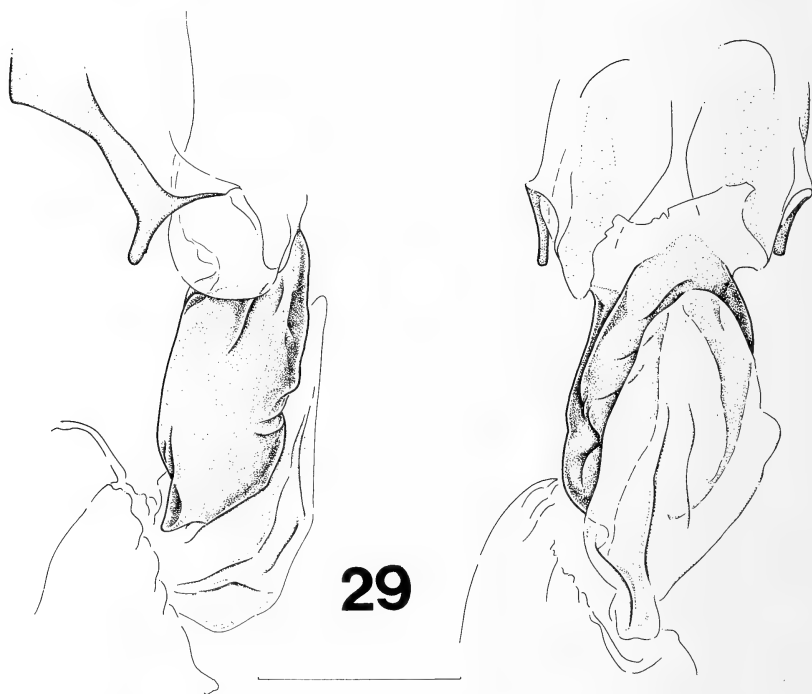


FIG. 29. Ductus bursae and portions of the corpus bursae and sterigma of the female genitalia of *Polites themistocles*, left lateral and ventral aspects. Williams Prairie, N. of Oxford, Johnson Co., Iowa, 28 May 1971, S. Miller (genitalia dissection no. 6052-CDM). Bar equals 1 mm.

arm is sinuate, not straight as in *margaretae*, and the anterior arm clearly extends as a wide spot across space 7. *Forewing length*: Left forewing 13.0 mm (paratypes 11.75–13.75 mm, $n = 13$).

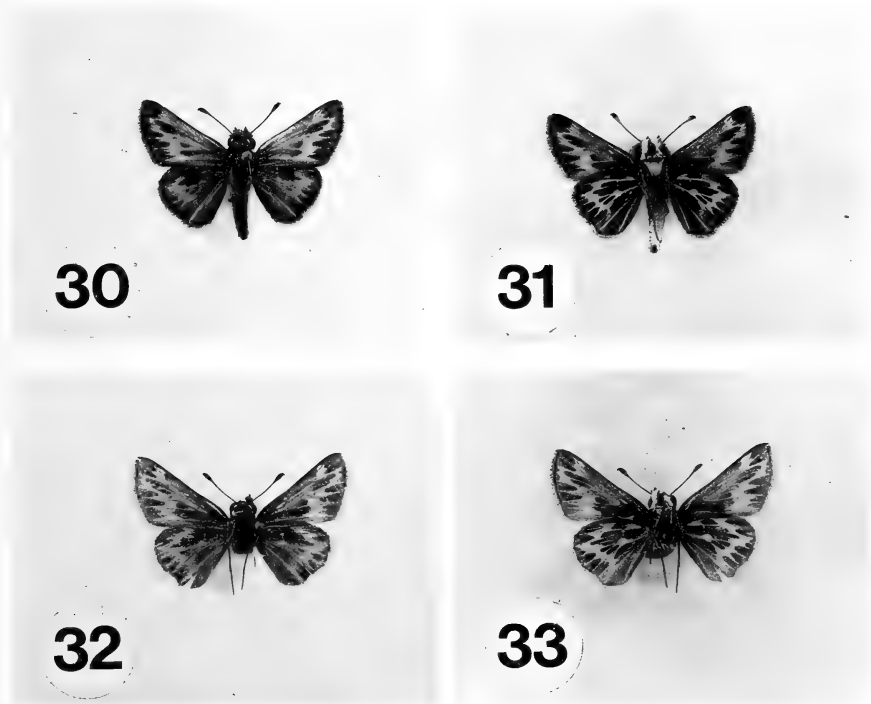
Abdomen: Ventrally buff, laterally with ochre hairs and scales, dorsally black with gold hairs cephalad. *Genitalia*: Penis slender, coecum penis slightly longer than mid-aedeagus width laterally, moderately reflexed ventrally cephalad, rostellum of unequal length, and with two sclerotized, multidentate cornuti, one conical and one tented and nearly or quite rectangular in side view. Tegumen in dorsal view broader than in *sabuleti* and taper of uncus to caudal tip relatively abrupt as in *margaretae*, terminal cleft longer than in *margaretae*. Valvae with a much more prominent "chin" caudally on the valvula in lateral aspect than in *margaretae*.

Female. Head, thorax, and abdomen as in male except for wing and genitalia.

Wing: Forewing longer, narrower and slightly more pointed apically than in *margaretae*. Markings as in male but the two discal, oval brown spots in spaces 1b and 2 larger and that in space 1b extends prominently to the base above. Hindwing above with the fulvous ray through cell more prominent than in male. Lower surface as in male but pale spot of anterior arm of macular band in space 7 larger. *Forewing length*: Left forewing 13.75 mm, 14.5 mm ($n = 2$ paratypes).

Genitalia: Ductus bursae relatively unwrinkled; ventral pouch small, little sclerotized; dorsal fold narrow, conspicuous.

Holotype. Male. MEXICO: Sonora, Bacochibampo Bay, vicinity Guaymas, IV-21-88;



FIGS. 30–33. Adults of *Polites norae* from Bacochibampo Bay, Sonora, MEXICO (even numbers upper side, odd numbers lower side; all $\times 1$); **30, 31**, Holotype male; **32, 33**, Paratype female (genitalic dissection no. 6044-CDM).

C. D. MacNeill and N. MacNeill-Maness, collectors. Deposited in the California Academy of Sciences, San Francisco (CAS).

Paratypes. Twelve male and two female paratypes same data as holotype except as follows: one male and one female IV-20-88, the female genitalia no. 6044 C. D. MacNeill, 1991; one male genitalia no. 6025, and one female genitalia no. 6035, both C. D. MacNeill, 1991; four males IV-22-88, three with genitalia nos. 6010, 6012, 6013, all C. D. MacNeill, 1991. One male, Guaymas, Mex(ico), April 13, 1921, E. P. VanDuzee, collector, genitalia no. 3986 J. H(errera), 1982. One male, San Carlos Bay, Sonora, Mexico, XII-22-35, Fred H. Rindge, collector. One male Mazatlan, Sinaloa, Mex(ico), Dec(ember) (19)16, J. August Kusche. Two male paratypes in the National Museum of Natural History, Smithsonian Institution (USNM), two male paratypes American Museum of Natural History (AMNH). Two male paratypes in the California Academy of Sciences, San Francisco (CAS), one male paratype in the Allyn Museum of Entomology (AME), and temporarily, the remaining five male and two female paratypes in the collection of C. D. MacNeill.

A specimen from San Carlos Bay, in Sonora, Mexico, was cited (as a female) by Austin (1987) as having a similar phenotype to *P. sabuleti margaretae*. That specimen is the San Carlos Bay male paratype cited above. *Polites norae* may easily be distinguished from *P. sabuleti margaretae* by the complete lack of a stigma in males, by the suggestion

of a fulvous ray through the cell of the hindwing above, and below by the wider angle of the macular band chevron (more acute in *margaretæ*), the lower arm of which is more sinuate while the upper arm is extended across space seven (compare Figs. 31, 33 with figs. 4, 6 in Miller & MacNeill 1969). In the male genitalia of *noræ*, the valvula of the valva has a prominent "chin" in lateral aspect, and the larger cornutus tends to be more rectangular. Females have a nearly wrinkle-free ductus bursae.

The species appears to be almost restricted to the upper intertidal zone of maritime marshes and just above. This zone seems to be dominated by one of two grasses, *Monanthochloe littoralis* Engleman (Poaceae) (Oakland Museum voucher #048820), a low growing, very prickly-looking carpet that doesn't much resemble a grass, or the related salt grass *Distichlis spicata* var. *stricta* (A. Gray) Beetle (Poaceae) (Oakland Museum voucher #048821), the presumed larval food plant (both grasses determined by Alan R. Smith, U.C. Berkeley Herbarium). Most of the accessible coastal marshes from just east of Guaymas north to Bahia Kino were checked for this skipper and for *Distichlis*. *Monanthochloe* was abundant and widespread in the marshes. A few marshes supported some *Distichlis*, usually near an at least ephemeral, fresh water stream. The type locality was the only brackish lagoon examined having a flowing fresh water input as well as a good stand of cattails (*Typha* sp?) (Typhaceae). The skippers were found with the grass well out into the upper intertidal region and also a short distance upstream above tidal reach. None was seen to nectar feed. A substantial brackish marsh with cattails was seen near Empalme, just east of Guaymas, but was inaccessible.

The grass at the type locality was grazed and trampled by small herds of cattle that were often driven through. These sites also served as dumps for copious debris and chemical wastes. These places seem to be waste repositories to the local people, and developers are evidently impressed with the potential for homes and resorts around these lagoons, which are eventually dredged and otherwise modified to accommodate marinas. Although there are still miles of coastline with maritime marshes along western Mexico, those with substantial freshwater input, once they become accessible, are in serious jeopardy of extreme modification owing to chemical contamination and development. While this may take decades, I am alarmed by the extent of change in these marshes (Guaymas, Bacochibampo Bay, San Carlos Bay, and Playa de los Algodones) that occurred between my visits during the 1970's and that of 1988. I suspect that this skipper cannot long survive the progress of humankind.

ACKNOWLEDGMENTS

I am indebted to my daughter Nora who was good company, who collected most of the type series in 1988, and for whom this species is named. For the loan of specimens, I thank Edward S. Ross (CAS), John Burns (USNM) and Fred Rindge (AMNH). For the excellent drawings I thank Shannon Bickford. George Austin and John Burns critically reviewed the manuscript and offered helpful suggestions for which I am grateful. For partial financial support I want to acknowledge the Entomology Department of the California Academy of Sciences.

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SIX SPECIES OF TIGER MOTHS
(ARCTIIDAE: LITHOSIINAE, CTENUCHINAE)
NEW TO THE UNITED STATES FAUNA, WITH
NOTES ON THEIR NOMENCLATURE AND
DISTRIBUTION IN MIDDLE AMERICA

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ABSTRACT. Six species of Arctiidae are reported from the United States (Texas and Arizona) for the first time, one in the subfamily Lithosiinae, *Rhabdatomis laudamia* (Druce), and five in the subfamily Ctenuchinae: *Apeplopoda mecrida* (Druce), **new combination**; *Eucereon myrina* Druce; *Eucereon erythrolepsis* Dyar; *Pseudosphex leovazquezae* (Pérez & Sánchez), **new combination**; and *Poliopastea clavipes* (Boisduval). Three of these species are also reported south of Mexico for the first time: *Apeplopoda mecrida* (Guatemala and Costa Rica); *Eucereon erythrolepsis* (Guatemala and Costa Rica); and *Pseudosphex leovazquezae* (Guatemala). Additional nomenclatural actions taken are: *Saurita improvisa* Schaus is transferred to *Apeplopoda* Watson, **new combination**; *Amycles strigosa* Druce is transferred from *Pseudosphex* Hübner to *Myrmecopsis* Newman, **new combination**.

Additional key words: Mexico, Guatemala, Costa Rica.

Moth collectors in the southwestern United States are continually discovering representatives of Mexico's rich tiger moth fauna not previously reported north of that republic. At least five of these recently were reported, without elaboration, from the United States for the first time by Franclemont (1983): *Gardinia anopla* Hering, *Eudesmia laetifera* (Walker), *Holomelina cetes* (Druce), *Ectypia mexicana* (Dognin), and *Turuptiana extrema* (Walker) [the last and *T. permaculata* (Packard) were transferred to *Hypercompe* by Watson and Goodger (1986: 29)]. I now report on the first U.S. occurrence of six additional species that have come to light in the course of routine curation, the study of other collections, and especially through the cooperation of several collectors who submitted their "mystery moths" for identification (see Acknowledgments section at the end of this paper for an explanation of the abbreviations used).

Where it is not intuitively obvious, I have indicated where these genera and species may be interpolated in the "MONA" Check List (Franclemont 1983). In the case of the Ctenuchinae, whose higher classification is virtually nonexistent, where one interpolates additional taxa is essentially arbitrary, as the present MONA Check List order follows neither that of Hampson (1898), Draudt (1915–1917), nor the scheme proposed by Forbes (1939). I also am taking this opportunity to update the nomenclature of the genera and species reported here,

as well as of those taxa already in the MONA Check List which are directly affected by the addition of the new records reported here.

ARCTIIDAE: LITHOSIINAE

Rhabdatomis laudamia (Druce, 1885)
(Fig. 1)

Lithosia laudamia Druce, 1885:131, pl. 13, fig. 4.

Crambidia laudamia (Druce): Kirby 1892:338.

Diarhabdosia laudamia (Druce): Hampson 1900:518, fig. 370; Draudt 1919:243, pl. 33, row h.

Rhabdatomis laudamia (Druce): Field 1964:53, figs. 13, 21, 22; Rindge 1965:3; Beutelspacher 1988b:892.

[Note: See Field (1964) for a more comprehensive synonymy.]

Specimen examined. ARIZONA: Santa Cruz Co., Santa Rita Mts., Madera Canyon, elev. 5000 feet [1525 m], 1 August 1965, Robert Crandall (1 male, LACM).

Distribution. The species has been reported from the Mexican states of Veracruz and Chiapas, south to Colombia (Beutelspacher 1988b:892, Field 1964:54, Rindge 1965:3). I have examined specimens from two additional states in MEXICO: San Luis Potosí: 5 km NE Ciudad del Maíz, elev. 4400 ft [1340 m], 8–10 May 1991, David G. Marqua (1 male, LACM). Oaxaca: Municipio Santiago Comaltepec, Puerto Eligio, elev. 650 m, 1 & 16 November 1980, Eduardo C. Welling M. (7 males, LACM); Municipio Santiago Comaltepec, Puerto Antonio, Sierra de Juárez, elev. 1200 m, 2 November 1980, Eduardo C. Welling M. (2 males, LACM).

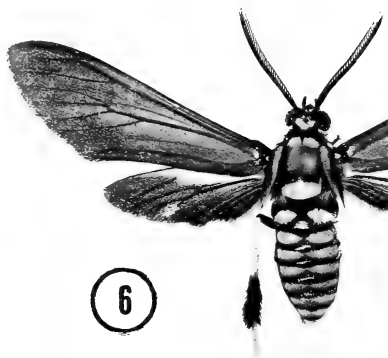
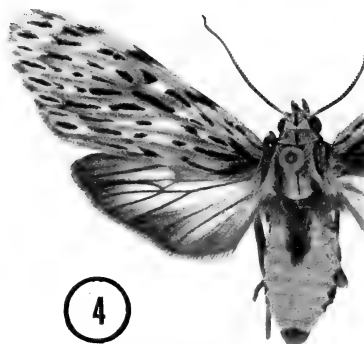
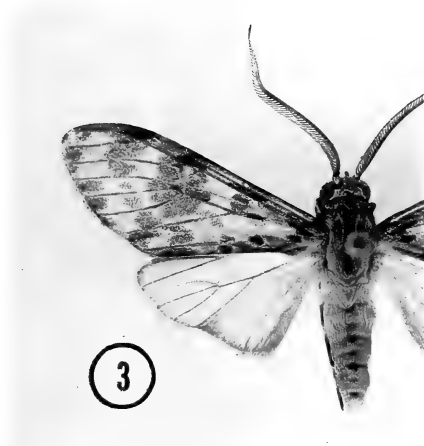
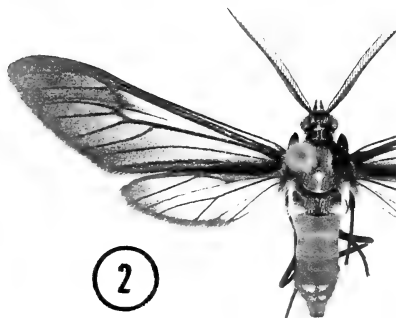
Remarks. This is the most puzzling of the new records reported here: not only is it the first and only specimen of this species ever taken, to my knowledge, in a locality that has been heavily collected for 50 years, but it is the most disjunct from its nearest known localities in central Mexico. At rest, this inconspicuous species resembles (and is presumably in a mimicry complex with) a lampyrid beetle, and for this reason may be overlooked by most collectors. *Rhabdatomis* Dyar, 1907, and its species *laudamia*, may be placed between *Lycomorpha* and *Hypoprepia* in the MONA Check List (Franclemont 1983).

ARCTIIDAE: CTENUCHINAE

Apeplopoda mecrida (Druce, 1889), **new combination**
(Fig. 2)

Gymnopoda mecrida Druce, 1889:84 (Type locality: Mexico City); Druce 1897:342, pl. 71, fig. 12; Kirby 1892:138.

Saurita mecrida (Druce): Hampson 1898:272; Zerny 1912:81; Draudt 1915:92, pl. 15, row e.



FIGS. 1-6. Arctiidae new to the United States fauna (FWL = forewing length): 1, *Rhabdatomis laudamia* (FWL = 9.5 mm); 2, *Apeplopoda mecrida* (FWL = 14.5 mm); 3, *Eucereon myrina* (FWL = 14.5 mm); 4, *Eucereon erythrolepis* (FWL = 16.5 mm); 5, *Pseudosphex leovazquezae* (female) (FWL = 11.0 mm); 6, *Poliopastea clavipes* (FWL = 14.5 mm).

Mystrocneme dulcicordis Dyar, 1907:51 (Type localities: Mexico City and Orizaba, Mexico); Zerny 1912:76.

Rhynchopyga dulcicordis (Dyar): Hampson 1914:181, pl. 9, fig. 24.

Saurita dulcicordis (Dyar): Draudt 1917:203, synonym of *Saurita mecrida*.

Specimens examined. ARIZONA: Cochise County: Douglas, 7 October 1945, W. W. Jones (1 female, LACM); Douglas, elevation 4000 feet [1220 m], 4 May 1986, UV light, P. M. Jump, Acc. #1040, (1 male, Jump collection).

Distribution. In addition to the type localities (Mexico City and Orizaba, Veracruz), and the Hidalgo specimens cited below (in Remarks), *Apeplopoda mecrida* has been reported from the city of Durango, Durango, Mexico (Druce 1897:342). I have examined the following additional specimens in the LACM collection from MEXICO: Mexico: Valle de Bravo, 24 July 1985, R. Turrent. Puebla: 2 km W of Cañada Morelos, 20 July 1976, E. Giesbert. Additionally, I have examined the first specimens to be reported south of Mexico, in Guatemala and Costa Rica, as follows (all in LACM):

GUATEMALA: Quezaltenango: Cantel, elev. 2200 m, 23 June 1987, E. C. Welling M.

COSTA RICA: Puntarenas Prov.: Monteverde, elev. 1400 m, 22–23 May 1974, E. Giesbert. Forbes (1939, 1942) did not record this species from Barro Colorado Island, Panama; montane Costa Rica may be the southern limit of distribution of the species.

Remarks. I was reluctant to report the 1945 capture of this species, thinking that it might have been mislabeled, but Jump's recent recollection of this moth in the same locality confirmed the much older record. With semi-hyaline brown wings and bright scarlet abdomen and thoracic dorsum, this wasp-like moth is unlike any other in the U.S.A., although it could possibly be confused at a glance with an aposematic/mimetic species of Zygaenidae (the family in which Druce first described it and in which Kirby cataloged it); the zygaenids, however, have chaetosemata and 2 anal veins in the forewing, among other differences.

Behavioral observations on the wasp-like ctenuchines, whether published or on label data, are scanty at best. In my personal experience some species are strictly diurnal while others are frequently taken at light; some may be both nocturnal and diurnal. *Apeplopoda mecrida* could be one of the latter. Jump (pers. comm.) reports that he took his specimen at 0730 h, MST, at rest about 5 feet [1.5 m] from his 15-watt fluorescent ultraviolet light; the moth was therefore quite possibly attracted to the light, perhaps as late as dawn, but still could have been a resting diurnal specimen within the search area of the collector. Diurnal activity of this species is, however, confirmed by at least one

of the three Mexican specimens, taken by butterfly collectors, that I have examined at CMNH. The field notes for a male (Hidalgo: 5 mi [8 km] N. Zimapán, 2140–2280 m, Sta. 17b, 12 January 1966, oak-piñon-juniper dense scrub, Clench & Miller CM-CUA Exp. 1966) indicate that the moth was diurnal, “apparently feeding on yellow *Senecio* flowers” [Asteraceae] (L. D. Miller specimen No. 1966-485). The other two specimens (1 male, 1 female), lacking behavioral data but presumably obtained in the course of routine diurnal butterfly collecting, also were taken on the same expedition in the state of Hidalgo: 4 mi [6.5 km] NE Jacala, 1740 m, Sta. 13, 10 January 1966, oak-juniper scrub (subhumid).

Apeplopora mecrida may be placed before *Cosmosoma* in the MONA Check List (Franclemont 1983).

Nomenclature. Watson (in Watson et al. 1980:14) proposed the replacement generic name *Apeplopora* for *Gymnopoda* Felder, 1874 (type species: *Gymnopoda ochracea* Felder, 1874), which is preoccupied by *Gymnopoda* Macquart, 1835 (Diptera). “*Saurita*” *mecrida*, clearly congeneric with what I have identified as *Apeplopora ochracea*, has been consistently misplaced since Hampson (1898:272) transferred it to *Saurita* (type species: *Sphinx cassandra* Linnaeus, a stout-bodied species with broad hind wings), based on the superficial similarity he found in a few external characters. Hampson did, however, segregate 6 species of *Saurita* (his section I), including *mecrida* and *ochracea*, on the basis of “Hind wing with the inner area very narrow,” but did not assign a genus-group name to this assemblage. I have not examined the remaining 4 species in this group [“*Saurita*” *cryptoleuca* (Walker), *biradiata* (Felder), *tristissima* (Perty), and *tenuis* (Butler)], so their formal transfer to another genus (or genera) would be premature, considering the present uncertainty of ctenuchine classification.

I have, however, examined specimens of the Costa Rican species *Saurita improvisa* Schaus (1912:36), described since Hampson’s monograph, and find it to be congeneric with *Apeplopora ochracea*, and consequently transfer it to that genus: *Apeplopora improvisa* (Schaus), **new combination**.

Eucereon myrina Druce, 1884

(Fig. 3)

Eucereon myrina Druce, 1884:84, pl. 9, fig. 10 (Type locality: Guatemala: [Baja Verapaz]: San Gerónimo [Jerónimo]); Kirby 1892:199; Druce 1897:362; Hampson 1898:508; Beutelspacher 1988a:471.

Eucereon myrina (Druce): Zerny 1912:141; Draudt 1915:180, pl. 25, row g. [Note: *Eucereon* Zerny (1912:137) is an unjustified emendation of *Eucereon* Hübner; see Watson et al. 1980:67.]

Eucereon aff. *myrina* (Druce): Beutelspacher 1982:409.

Eucereon aff. *myrina* (Druce): Beutelspacher 1982:fig. 13.

Euceron [sic] *myrina* (Druce): Beutelspacher 1988a:466. [Note: *Euceron* is an incorrect subsequent spelling of *Eucereon* Hübner.]

Specimens examined. ARIZONA: Cochise Co.: Huachuca Mts., Ash Canyon, 5100 feet [1555 m], 27 July (1 male) & 3 August (1 female) 1981, N. McFarland (LACM); Huachuca Mts., mouth of Miller Canyon, 5000 feet [1524 m], 6 September 1970, C. Henne (1 male, LACM). Pima Co.: Santa Rita Mts., N end, Rosemont Area, 31°48–53'N, 110°42–47'W, UV light, Ridge Area, Sec. 36 [?-second digit obliterated by pin hole], elev. 5600 feet [1700 m], Anamax Mine Inventory, 11 August 1975, J. Busacca & C. Olson (1 male, Univ. of Arizona, Tucson). Santa Cruz Co.: Santa Rita Mts., Madera Canyon, 5000 feet [1524 m], 2 August 1981, R. Leuschner (1 female, Leuschner collection); same locality, 10 August 1981, R. Crandall (1 male, LACM).

Distribution. *Eucereon myrina* is common and widespread in Mexico; I have seen specimens from Sonora, Sinaloa, Jalisco and Baja California Sur on the west and San Luis Potosí on the east, south to Chiapas. The species was described from Guatemala, but I have not seen any specimens from there or any farther south.

Nomenclature. See comments under *Eucereon erythrolepsis*.

Eucereon erythrolepsis Dyar, 1910

(Fig. 4)

Eucereon erythrolepsis Dyar, 1910:232 (Type locality: Mexico: [Veracruz]: Cordoba) (holotype female in USNM, examined).

Eucereon [sic] *erythrolepe* [sic] (Dyar): Zerny 1912:139. [Note: *Eucereon* Zerny (1912: 137) in an unjustified emendation of *Eucereon* Hübner; see Watson et al. (1980:67).]

Eucereon erythrolepsis [sic] Dyar: Hampson 1914:331, as junior subjective synonym of *Eucereon pilati*[i] Walker, in error. [Note: *erythrolepsis* is an incorrect subsequent spelling of *erythrolepsis*.]

Eucereon [sic] *erythrolepsis* (Dyar): Draudt 1915:176, pl. 25, row b.

Euceron [sic] *erythrolepsis* (Dyar): Beutelspacher 1988a:466. [Note: *Euceron* is an incorrect subsequent spelling of *Eucereon* Hübner.]

Euceron [sic] *erythrolepsis* (Dyar): Beutelspacher 1988a:469. [Note: *Euceron* is an incorrect subsequent spelling of *Eucereon* Hübner.]

Specimen examined. TEXAS: Webb Co., Laredo, 20 September 1971, T. W. Taylor, 1 female [LACM].

Distribution. *Eucereon erythrolepsis* has hitherto only been known from Mexico; I have examined specimens from the states of Sinaloa (July, August, December), San Luis Potosí (May), Quintana Roo (July–October), and Veracruz (July). Additionally, I report here the first records south of Mexico, from Guatemala (three departamentos) and Costa Rica (all in LACM):

GUATEMALA: Alta Verapaz: Finca El Salto, 2 km N Tukurú, 19°00'N, 90°07'W, elev. 320 m, moist forest, 11–21 May 1991, Peter Hubbell (1

female, LACM). Jutiapa: Finca Cerro Gordo, 11 km S Moyuta, elev. 515 m, 14–18 July 1991, Peter Hubbell (3 males). Zacapa: La Unión, 850 m, 12 September, 3 November, and 10 December 1972, E. C. Welling M. (3 males); 3 km E La Unión, cloud forest at 1540 m, 12–17 August 1991, Peter Hubbell (1 female).

COSTA RICA: Puntarenas Province, Monteverde [ca. 1400 m], 16 June 1972, C. L. Hogue & J. Dockweiler (1 female).

Remarks. *Eucereon erythrolepsis* is very similar in size and appearance to the sympatric *E. pilatii* Walker, 1854 (frequently misspelled “*pilati*”; type locality Honduras), a species I have seen from as far north as San Luis Potosí, Mexico, and which may eventually be discovered in Texas. The two may be distinguished as follows: in *E. erythrolepsis* the forewing ground color is usually grayish; the largest rectilinear spot on the forewing is in the lower distal end of the discal cell; the red abdomen is dorsally unspotted posterad of the dark brown basal patch (but apex of abdomen is black in both species); and the male genitalia have a broad, spoon-shaped valva, a simple uncus, and a stout, dorso-ventrally curved, paired superuncus. In *E. pilatii* the forewing ground color is brown; the largest rectilinear forewing spot is *below* the end of the discal cell, in cell Cu_1 - Cu_2 ; each abdominal segment posterad of the basal patch has a middorsal black spot; and the male genitalia have a slender valva abruptly terminating in a sharp point, a massive Y-shaped uncus, and a paired superuncus of long, curved, slender, pointed arms. The figures of both species in my copy of “Seitz” (Draudt 1915: pl. 25, row b) are very poor, but do accurately depict the dorsal abdominal differences.

Nomenclature. *Eucereon* is a large, heterogeneous genus badly in need of revision. Several genera have been resurrected from the synonymy of *Eucereon*, including *Theages* Walker (Travassos 1962, 1964) and *Galethalea* Butler (Travassos 1952a). The sole species of *Eucereon* previously listed for the North American fauna (*carolina*) actually belongs to *Nelphe*, another former synonym of *Eucereon* that has been resurrected (Travassos 1952b, 1952c). (Complete bibliographic and type species information for these genera may be found in Watson et al. 1980.) A revised synonymy for *Eucereon* and *Nelphe*, and their species in America north of Mexico (in MONA Check List format), would be:

EUCEREON Hübner, [1819] 1816

ERITHALES Poey, 1832

EUCEREEON Walker, 1854 [misspelling]

EUCEREA Walker, 1856 [misspelling]

ACRIDOPSIS Butler, 1876

EUCEREUM Zerny, 1912 [unjustified emendation]

EUCERON Beutelspacher, 1988 [misspelling]

EUCERERON Beutelspacher, 1988 [misspelling]

8270.1 *myrina* Druce, 1884

8270.2 *erythrolepis* Dyar, 1910

erythrolepis Hampson, 1914 [misspelling]

NELPHE Herrich-Schäffer, [1858] 1850–1858

8271 *carolina* Hy. Edwards, 1886

confinis (Druce, 1884), not H.-S. [misident.]

confine (Hampson, 1898), in part, not H.-S.

cubensis (Schaus, 1904)

Pseudosphex leovazquezae (Pérez & Sánchez, 1986),

new combination

(Fig. 5)

Abrochia leovazquezae Pérez & Sánchez, 1986:234 (Type locality: Mexico: Veracruz: Cerro

Specimens examined. TEXAS: Hidalgo Co., Santa Ana Refuge, 13 November 1971 (1 female); same locality, 23 September 1973 (1 male); both specimens collected by A. & M. E. Blanchard (USNM).

Distribution. *Pseudosphex leovazquezae*, described from Veracruz, Chiapas, and San Luis Potosí, frequently is taken at lights in eastern Mexico. I have examined approximately 100 specimens from the following states (arranged north to south) and months (collections of USNM, R. B. Nagle, E. C. Knudson, CNC, CMNH, UCB and LACM): Nuevo León (July), Tamaulipas (June, July); San Luis Potosí (March, May–August, October, November); Veracruz (June, August); Oaxaca (July, September, November); Chiapas (May); and Quintana Roo (June–December).

This species has not been previously reported south of Mexico. I have examined a single specimen from GUATEMALA: Jutiapa: Finca Cerro Gordo, 11 km S Moyuta, elev. 515 m, 14–18 July 1991, Peter Hubbell (1 female, LACM).

Remarks. This recently described species is remarkably similar in appearance to over a score of wasplike Neotropical species in several diverse genera. Species of *Pseudosphex* may be readily distinguished from similar-appearing genera by having a large, fully developed hind-wing discal cell with only three posterior veins (vein M_2 absent). A very similar species, to be described later, is widely distributed in Mexico, principally on the Pacific Slope.

Nomenclature. Although the genus *Pseudosphex* is already included in the North American fauna (Franclemont 1983:119), the species placed in it actually belongs in another genus. The confusion arose when Hampson (1898:154), followed by Draudt (1915:38), wrongly consid-

ered the type species of *Pseudosphex* to be *Pseudosphex polistes* Hübner, instead of *Pseudosphex zethus* Hübner, with the result that their concept of *Pseudosphex* is actually *Myrmecopsis* Newman. The species they placed in *Chrysostola* and *Abrochia*, respectively, belong in *Pseudosphex*. Complete bibliographic and type species information for these genera may be found in Watson et al. (1980). A revised synonymy for these two genera and their species in America north of Mexico (in MONA Check List format) would be:

PSEUDOSPHEX Hübner, 1818

SPHECOMORPHA Hübner, 1808 [rejected]

SPHECOMORPHA Hübner, 1818 [unavailable]

ABROCHIA Herrich-Schäffer, 1855

CHRYSOSTOLA Herrich-Schäffer, [1855]

SPHECOPSYCHE Dognin, 1898

PSEUDARGYROEIDES Klages, 1906

PSEUDARGYROIDES Zerny, 1912 [unjustified emendation]

8276.1 **leovazquezae** (Pérez & Sánchez, 1986)

MYRMECOPSIS Newman, 1850

SPHECOPSIS Felder, 1874

PSEUDOSPHEX of authors, not Hübner, 1818

8277 **strigosa** (Druce, 1884) (*Amycles*), **new combination**

Poliopastea clavipes (Boisduval, 1870)

(Fig. 6)

Mastigocera clavipes Boisduval, 1870:81 (Type locality: Mexico).

Mastigocera calvipes [sic] (Boisduval): Druce 1884:49, pl. 6, fig. 20; Druce 1897:339.

[Note: *calvipes* is an incorrect subsequent spelling of *clavipes*.]

Drucea clavipes (Boisduval): Kirby 1892:130.

Horama clavipes (Boisduval): Hampson 1898:420; Draudt 1915:143, pl. 21, row i; Zerny 1912:121.

Poliopastea clavipes (Boisduval): Dietz & Duckworth 1976:22, figs. 10–12, pl. 3, figs. 17–18; Beutelspacher 1984:172, 179, fig. 19; Beutelspacher 1988a:464.

Specimen examined. TEXAS: Hidalgo Co., Santa Ana Wildlife Refuge, 28 October 1986, E. C. Knudson (1 male, Knudson collection).

Distribution. Widespread and frequently collected in Mexico, reported as far south as Venezuela (Hampson 1898:420); melanic specimens may be confused with other species (see Remarks). In the course of this study I have examined specimens from the Mexican states of Colima, Michoacán, Quintana Roo, San Luis Potosí, and Sinaloa.

Remarks. This moth may be overlooked because of its resemblance to the more common *Horama panthalon texana* (Grote). *Poliopastea clavipes* is variable in coloration; although it is the only non-black member of the genus, melanic specimens are common (but all specimens

retain the iridescent metallic spots and the white antennal tips). Completely black specimens resemble *P. laconia* (Druce), while black specimens with orange hind tarsi resemble *P. laciades* (Schaus); in fact, "normal" yellow/brown specimens of *P. clavipes* look very similar to these two species when photographed under ultraviolet light (Dietz & Duckworth 1976:22, pl. 3, figs. 17, 18). Forbes (1939:131) noted that *P. laconia* and *P. laciades* appeared to have identical male genitalia, and speculated that the two species may merely be color forms of each other, while Dietz and Duckworth (1976:22) observed that the male genitalia of *P. laciades* and *P. clavipes* also appeared identical, and suggested the possibility of a polymorphic species, an hypothesis supported by my examination of scores of specimens from Mexico and Guatemala. All three "species" are sympatric over much or all of their ranges. *Poliopastea* is clearly in need of revision; until then, however, some simple rearing experiments to ascertain the number of "species" among the offspring of a single parent female would aid significantly in the resolution of the polymorphism question.

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Numerous individuals and institutions have assisted in this study by drawing my attention to new records, through the loan or gift of specimens, and by providing access to the collections in their care. Institutions, their abbreviations as used in this paper, and their curators include CMNM (Carnegie Museum of Natural History, J. E. Rawlins); CNC (Canadian National Collection, Agriculture Canada, J. D. Lafontaine); LACM (Natural History Museum of Los Angeles County); UCB (University of California, Berkeley, J. A. Powell); USNM (U.S. National Museum of Natural History, Smithsonian Institution, D. C. Ferguson & R. W. Hodges). I thank the following individuals for their generous cooperation: R. Crandall, P. M. Jump, R. H. Leuschner, R. B. Nagle, and T. W. Taylor; E. C. Knudson deserves special mention: not only did he discover one third of the records reported here, but his initial inquiry about the identity of what was then an undescribed species of *Pseudosphex* launched my project to catalog and study the Neotropical Ctenuchinae. Some of the LACM specimens cited in this paper were prepared and curated with the aid of two collection improvement grants from the National Science Foundation (BSR-8410742 and BSR-8800344), which are gratefully acknowledged. My thanks to Don Meyer for cheerfully executing the photographs and to Brian P. Harris for technical assistance.

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CLADISTIC ANALYSIS OF THE GENERA OF THE SUBFAMILY ARSENUURINAE (SATURNIIDAE)

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ABSTRACT. The Neotropical saturniid subfamily Arsenurinae contains about 60 species in ten genera. Hypothetical phylogenies of the ten genera were constructed using cladistic methodology to analyze morphological characters of adults and larvae. Based on the resultant cladograms, *Titaea* and *Dysdaemonia* are sister-groups, and this pair may be the sister-group of *Paradaemonia*. These three are probably the sister-group to *Caio* and possibly to *Arsenura*. *Copiopteryx* and *Rhescyntis* are sister-groups based on the suite of characters used. Other relationships are less certain from the available data; larvae of three genera are not known. At least four genera are specialists on Bombacaceae as larval hostplants, but several other plant families are used by species in the other genera evaluated. Arsenurinae appears to be a relict group represented by relatively few species and genera.

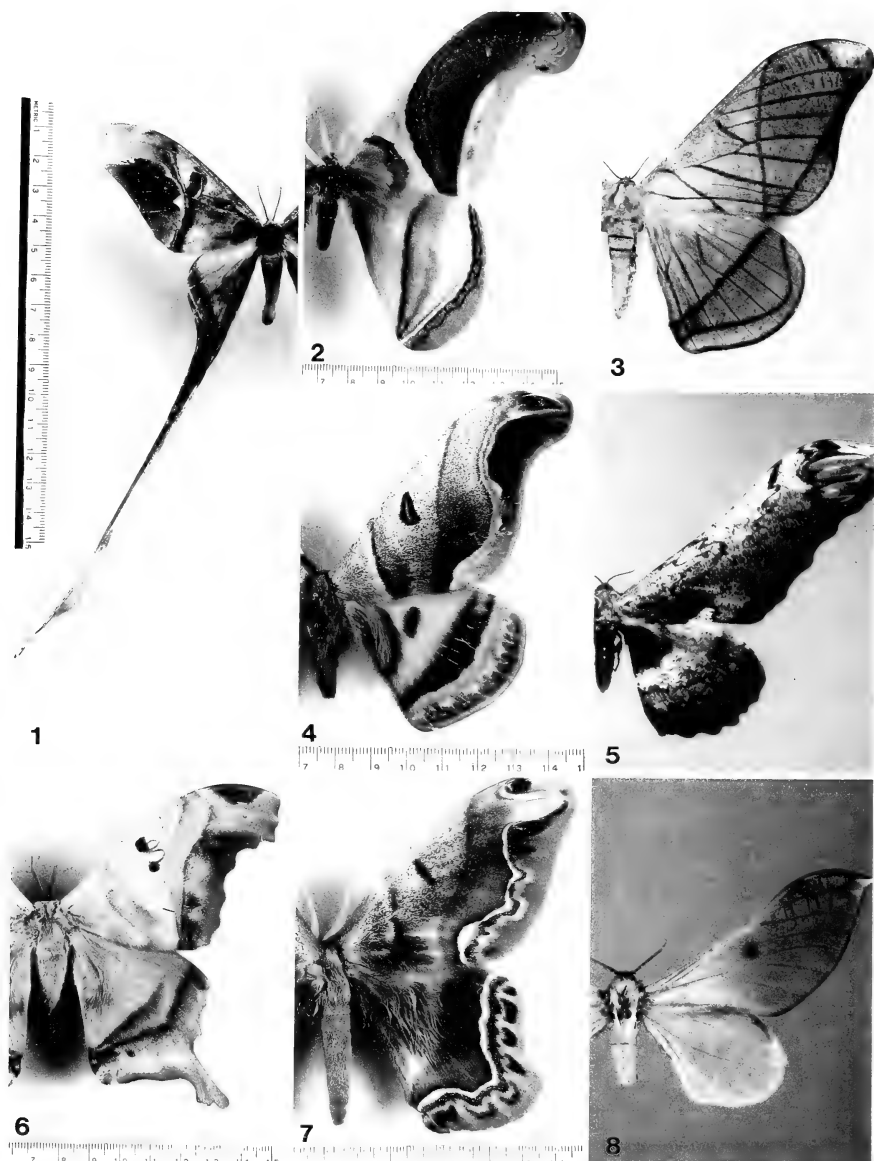
RESUMEN. La subfamilia Arsenurinae de las Saturniidae tiene cerca de 60 especies en diez géneros, todos en la región neotropical. Se empleó la metodología cladística para ilustrar las filogenias hipotéticas de los diez géneros. *Titaea*, *Dysdaemonia*, y *Paradaemonia* son grupos afines, juntos probablemente con *Caio* y *Arsenura*. *Copiopteryx* y *Rhescyntis* son grupos afines basado en el juego de características usado. Otras relaciones son menos ciertas con los datos existentes. Las orugas de cuatro o más géneros son fitófagas especialistas sobre la familia Bombacaceae, pero otras familias de plantas son huéspedes para los demás géneros de Arsenurinae. Esta subfamilia es un grupo relicto que está representado para pocos especies y géneros.

Additional key words: systematics, phylogeny, morphology, early stages, Neotropical.

The Neotropical saturniid subfamily Arsenurinae includes approximately 60 species ranging from northern Mexico to northern Argentina (Lemaire 1980). The moths are large to very large, and their coloration is restricted to earth tones, mainly shades of brown, gray, cream, and dull orange (Figs. 1-8). In the revisionary works of Michener (1952) and Ferguson (1971-72), the name Rhescyntinae was used for this group. Lemaire (1980) published a definitive treatment of the subfamily, providing details on classification, synonymy, morphological characters, and distribution of each species. Relationships between the ten genera have not been proposed except for a superficial "tree" in Michener's (1952) work, and the fact that Lemaire (1980) separated the genus *Almeidaia* into a separate tribe. Strecker (1875:101) also offered some brief, yet insightful, comments on relationships within this group.

MATERIALS AND METHODS

This cladistic analysis presupposes that all ten genera of the subfamily were correctly defined by Lemaire (1980) (see Table 1). Michener (1952) classified the species of *Caio* under *Arsenura*, and grouped *Arsenura* along with *Rhescyntis*, *Dysdaemonia*, *Titaea*, and *Paradae-*



FIGS. 1-8. 1, *Coptiopteryx semiramis* (Cramer), Rancho Grande, Aragua, Venezuela; 2, *Rhescyntis pseudomartii* Lemaire, Itatiaia, Santa Catarina, Brazil; 3, *Grammopelta lineata* (Schaus), Anchicaya, Valle, Colombia; 4, *Caio romulus* (Maassen), Itatiaia, Santa Catarina, Brazil; 5, *Loxolomia johnsoni* Schaus, Sinop, Mato Grosso, Brazil; 6, *Titaeta tamerlan* (Maassen), Colombia; 7, *Arsenura biundulata* Schaus, Rio Vermelho, Santa Catarina, Brazil; 8, *Almeidaia romualdoi* Travassos, Rio Verde, Mato Grosso, Brazil.

TABLE 1. Genera of Arsenurinae.

Genus	Type-species	No. of known species
<i>Arsenura</i> Duncan	<i>armida</i> (Cramer)	ca. 23
<i>Caio</i> Travassos & Noronha	<i>romulus</i> (Maassen)	4
<i>Dysdaemonia</i> Hübner	<i>boreas</i> (Cramer)	3
<i>Titaea</i> Hübner	<i>orsinome</i> Hübner	4
<i>Paradaemonia</i> Bouvier	<i>pluto</i> (Westwood)	12
<i>Rhescyntis</i> Hübner	<i>hippodamia</i> (Cramer)	4
<i>Copiopteryx</i> Duncan	<i>semiramis</i> (Cramer)	5
<i>Loxolomia</i> Maassen	<i>serpentina</i> Maassen	2
<i>Grammopelta</i> Rothschild	<i>lineata</i> (Schaus)	1
<i>Almeidaia</i> Travassos	<i>romualdoi</i> Travassos	2

monia as five subgenera of *Rhescyntis*. Subgeneric usage is well established in Hymenoptera taxonomy where the majority of Michener's contributions are found, but subgenera receive much less usage in Lepidoptera taxonomy. With the exception of *Caio*, the generic groupings of Lemaire and Michener are in agreement and I accept them as monophyletic groups. The purpose of this paper is to propose hypotheses of the phylogeny of these genera through the construction of cladograms. The works of Michener and Lemaire provide ample data on the morphology of the adults of each genus, and the present study incorporates available information on the immature stages, using published life histories (Schreiter 1925, Travassos & d'Almeida 1937, Travassos 1946, Lordello & Mariconi 1953, Otero 1965, d'Almeida 1975, Dias 1978, Brenner & Lampe 1987) and larvae preserved in alcohol. Preserved material of 1st instar larvae available to this study were: *Arsenura armida* (Cramer), *A. ponderosa* Rothschild, *A. polyodonta* (Jordan), *A. rebeli* Gschwandner, *Caio richardsoni* (Druce), *C. championi* (Druce), *Dysdaemonia boreas* (Cramer), *Titaea tamerlan* (Maassen), *Paradaemonia andensis* (Rothschild), *Rhescyntis* sp., and *Copiopteryx semiramis* (Cramer). Preserved mature caterpillars of several of these also were available.

Numbers of species listed in Table 1 differ from the revision of Lemaire (1980) for three genera as follows: 1) some of the so-called subspecies within *Arsenura* are considered by me to be full species; 2) what has been cited as *Caio undilinea* (Schaus) is apparently a form of the variable *C. championi* (Druce) (C. Lemaire, pers. comm.); 3) a second species of *Almeidaia* was described as *A. aidaie* by Mielke and Casagrande (1981).

Although American taxonomists and evolutionary biologists neither understood nor utilized cladistic theory and methodology until the 1960's and 1970's, the work of Michener (1952) actually employed

TABLE 2. Matrix of the 23 characters used to analyze the phylogeny for the ten genera. See text for explanation.

<i>Arsenura</i>	<i>Cato</i>	<i>Dysdaemia</i>	<i>Titaea</i>	<i>Paradaemia</i>	<i>Rhescyntis</i>	<i>Copiop- teryx</i>	<i>Loxolomia</i>	<i>Grammo- pelta</i>	<i>Almeidaia</i>
A	A	A	A'	A	A'	A'	A	A	A
B	B'	B'	B	B'	B	B	B'	B'	B
C''	C'	C'	C'	C'	C	C	C'	C'	C''
D	D	D	D	D	D'	D'	D	D	D
E	E	E'	E'	E'	E	E'	E	E	E
F'	F'	F'	F'	F'	F	F''	F	F	F
G'	G	G'	G'	G	G'	G	G	G	G
H	H	H'	H'	H	H	H'	H	H	H
I'	I'	I'	I'	I'	I'	I'	I'	I	I''
J'	J'	J''	J''	J''	J''	J''	J''	J	J
K'	K'	K'	K'	K'	K'	K'	K'	K'	K
L'	L	L	L	L	L'	L'	L'	L'	L'
M''	M''	M''	M''	M	M	M'	M'	M''	M
N''	N'	N''	N''	N''	N''	N	—	—	—
O	O''	O'	O'	O'	O'	O	—	—	—
P	P	P	P	P'	P'	P'	—	—	—
Q'	Q'	Q'	Q'	Q'	Q'	Q	—	—	—
R	R'	R	R	R	R	R	—	—	—
S	S	S	S	S'	S	S'	—	—	—
T	T'	T''	T''	T''	T''	T''	—	—	—
U	U'	U'	U'	U'	U'	U'	—	—	—
V	V'	V'	V'	V'	V'	V'	—	—	—
W'	W'	W'	W'	W	W	W	—	—	—

cladistic theory. This is clear from his discussions of out-group comparison in determining which characters were apomorphic (i.e., derived, advanced) and which plesiomorphic (i.e., ancestral, primitive). Methods in the present study are the same as those explained in detail in another cladistic analysis of the nine genera of the saturniid tribe Attacini (Peigler 1989); the reader is also referred to a succinct overview of cladistic methodology by Andersen (1978). The branching pattern is determined by the greatest number of shared apomorphies between each possible pair. The characters used in this analysis are discussed below and their distribution among taxa is shown in Table 2. A second cladistic method was applied to the data in Table 2 by the computer program PAUP (Phylogenetic Analysis Using Parsimony) (Swofford 1990), using the branch-and-bound search option. Characters E, F, H, O, P, S, and V were judged to have greater value and therefore counted twice in the PAUP analysis, and *Almeidaia* was designated as the out-group.

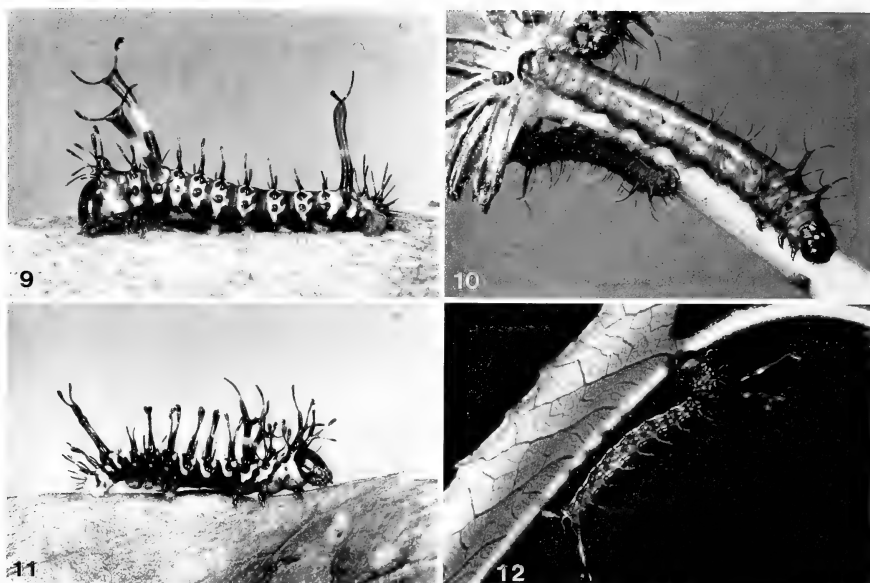
All authors agree that the Arsenurinae and Ceratocampinae (=Citheroniinae) are the most plesiomorphic subfamilies of Saturniidae (Michener 1952, Lemaire 1980, 1988), and some Brazilian authors have com-

bined the two under the family name Adelocephalidae. Although these two subfamilies are possibly sister-groups, the following shared characters probably include symplesiomorphies in the context of Saturniidae: female antennae simple, abdomen elongated, wing colors and patterns simple yet cryptic, discal spots better developed on forewing than on hindwing, larvae with elongated horns on meso- and metathoracic and 8th abdominal segments, pupation below ground without cocoon. Some of these characters are apomorphic in the context of the other Bombycoidea (Minet 1991), but a careful comparison with other bombycoid groups would be necessary to determine whether Ceratocampinae and Arsenurinae are sister-groups or simply two groups sharing several primitive characters (see Lemaire 1988:16). The two subfamilies differ in several characters of the legs (Oiticica 1940), wing venation, male antennae (Michener 1952), and larval structure (Packard 1905).

The two families that are possibly most closely allied to the Saturniidae are Cercophanidae and Oxytenidae (Michener 1952, Jordan 1924). In this study these two Neotropical families were used for out-group comparison with Arsenurinae, as well as the subfamily Ceratocampinae, other saturniid subfamilies, and other families in Bombycoidea. Minet (1986) proposed that the Cercophanidae as defined by Jordan and accepted by subsequent authors, may be a paraphyletic group and probably should be included in the Saturniidae. The saturniid subfamily Agliinae also possesses some plesiomorphic characters (Michener 1952), as seen in figures of the immature stages given by Kuroko (1976) and Gómez de Aizpúrua (1988). This study also uses concise morphological summaries of several families of Bombycoidea that were provided by Common (1990). The large, brown, Australian bombycoid moth *Chelepteryx collesi* Gray (Anthelidae) (Common 1990) bears a remarkable convergent resemblance in size, wing pattern, and color to some *Arsenura*. In light traps, *Arsenura* also closely resemble large Noctuidae (*Ascalapha* Hübner and *Thysania* Dalman) (C. Lemaire pers. comm.).

Immature Stages

Although little has been published on the immature stages of Arsenurinae, certain conclusions and sets of characters can be stated. It is particularly unfortunate that the 1st instar larvae of several groups remain unknown. These include Oxytenidae, *Loxolomia*, *Grammopelta*, and *Almeidaia*, the latter two of which are considered to be the most primitive arsenurine genera based on adult characters (Michener 1952, Lemaire 1980). When these larvae become known, their characters will either strengthen or modify the hypotheses of the phylogeny

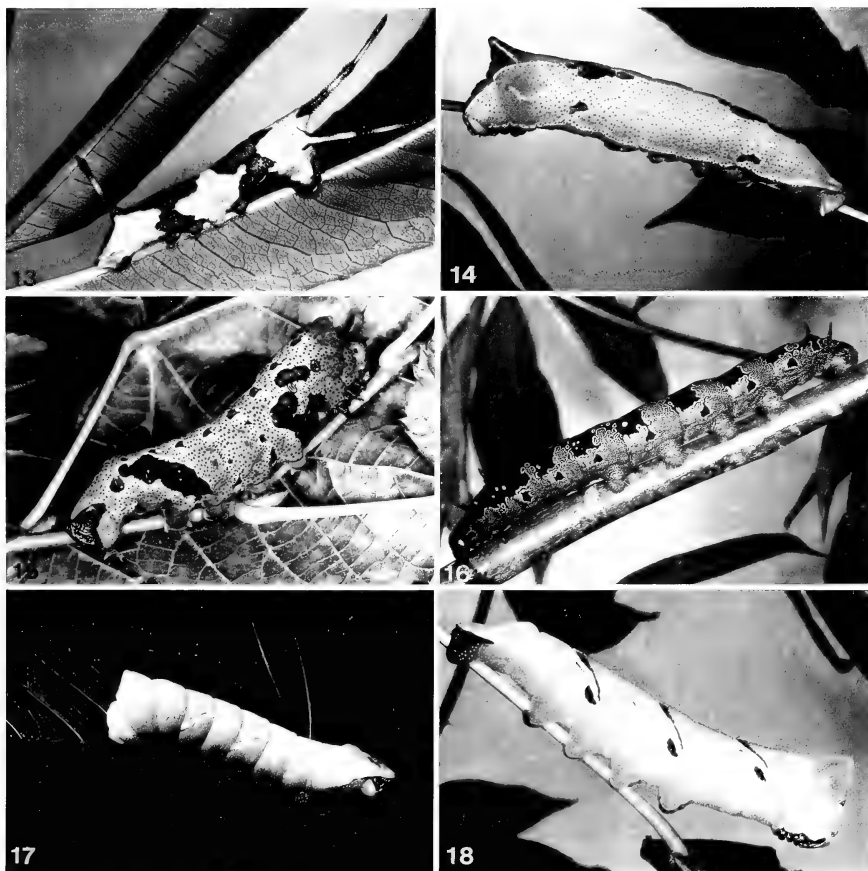


FIGS. 9–12. First instar larvae of Arsenurinae. 9, *Rhescyntis hippodamia* (Cramer), French Guiana; 10, *Arsenura polyodonta* (Jordan), Lake Chapala, Jalisco, Mexico; 11, *Paradaemonia* sp., French Guiana; 12, *Dysdaemonia boreas* (Cramer), Santa Rosa de Puriscal, Costa Rica.

proposed in the present paper. For example, *Loxolomia* and *Grammopelta* are probably not true sister-groups, but in the absence of larval characters, the four synapomorphies of the adults could not be ignored. Representative examples of larvae are presented in Figs. 9–18.

Form of larvae: Within the genera of the subfamily for which the mature larvae are known, there are two main forms: (1) gracile, weakly hirsute, with smooth integument (*Rhescyntis*, most *Arsenura*) (Fig. 16), and (2) stout, glabrous, with granulose integument (*Caio*, *Dysdaemonia*, *Copiopteryx*) (Figs. 14, 15, 17, 18). The latter form is considered plesiomorphic based on the presence of these characters in larvae of Cercophanidae (Packard 1914), Oxytenidae (Jordan 1924, Nentwig 1985), Agliinae (Kuroko 1976, Gómez de Aizpúrua 1988), and most Ceratocampinae (Lemaire 1988). Form of larvae was not used in the present analysis because it cannot be discretely quantified nor qualified.

Larvae of certain arsenurines bear a striking but convergent resemblance to notodontid larvae such as the Palearctic *Cerura vinula* (L.) and the Nearctic *Cerura scitiscrypta* Walker (see Gómez de Aizpúrua 1988, Nässig 1988). The tentacles and the peculiar brown and green pattern shared by these Arsenurinae and Notodontidae evidently impart the same protective function, probably simulating a rolled or twisted



FIGS. 13–18. Larvae of Arsenurinae. 13, 14, *Dysdaemonia boreas* (Cramer), third and fifth instars, Santa Rosa de Puriscal, Costa Rica; 15, *Titaea tamerlan* (Maassen), fifth instar, State of Rio de Janeiro, Brazil; 16, *Arsenura polyodonta* (Jordan), fifth instar, Lake Chapala, Jalisco, Mexico; 17, *Caio championi* (Druce), fifth instar, Santa Rosa National Park, Guanacaste, Costa Rica; 18, *Caio richardsoni* (Druce), fifth instar, Sonora, Mexico.

leaf (see also Nentwig 1985). This category includes the full-grown larva of *Rhescyntis* (Travassos & d'Almeida 1937) which lacks tentacles, although its laterally flattened form may also mimic a legume seed pod. The mature larvae of *Cercophana frauenfeldi* Felder (Cercophanidae) (Packard 1914, pl. 31) also resembles a seed pod and the larva of *Rhescyntis*. In contrast to these examples of camouflaged forms, larvae of several *Arsenura* are aposematic, colored black and orange. These probably derive and sequester toxic substances from their hostplants.

Structure of 1st instar larvae: In all 11 species in seven genera of Arsenurinae for which 1st instar larvae were examined, the crochets

are in the form of a uniordinal mesoserries. In all mature larvae examined, these form biordinal or triordinal mesoserries. The same is true in the genus *Aglia* Ochsenheimer for larvae of the 1st and 4th (the last in *A. tau* (L.) according to Packard 1914, and R. Oberprieler pers. comm.) or 5th (the last in *A. microtau* Inoue according to Kuroko 1976) instars. These observations verify the prediction by Pease (1961:101) that older larvae would be found to have more crochets.

All species have enlarged bifid dorsal scoli on the metathorax. Likewise, no useful characters were found on the abdominal segments. However, the dorsal and subdorsal scoli on the prothorax and mesothorax vary widely and appear to be valuable in phylogenetic analysis. Again, the Palearctic *Aglia* agrees in having very large dorsal scoli on the prothorax and metathorax, and greatly reduced mesothoracic ones. In the Brahmaeidae, the prothoracic scoli are reduced (Packard 1914, pl. 34). In 1st instar Ceratocampinae, some genera have hypertrophic dorsal scoli on all three thoracic segments (e.g., *Citheronia* Hübner and *Eacles* Hübner, some of the most primitive genera according to Michener 1952), others on the mesothorax and metathorax only, others (e.g., *Anisota* Hübner) only on the mesothorax (Packard 1905). The structure of prothoracic scoli provides strong support for the separation of *Caio* from *Arsenura*.

Hostplants: No hostplants have been reported for *Loxolomia*, *Grammopelta*, or *Almeidaia*. For the other seven genera, *Rhescyntis* uses nutmeg (*Virola*, Myristicaceae); *Copiopteryx* uses Sapotaceae and Santalaceae; *Paradaemonia* uses Lythraceae; and *Caio*, *Dysdaemonia*, and *Titaea* apparently specialize on Bombacaceae. The large genus *Arsenura* uses several families in addition to Bombacaceae. Specific hostplant records are tabulated in Table 3. Bombacaceae, Tiliaceae, Malvaceae, and Sterculiaceae belong to the order Malvales (Lawrence 1951). Utilization of this plant group may be plesiomorphic for Arsenurinae since some Cercophanidae feed on Tiliaceae (Jordan 1924), but the phylogeny proposed below suggests that specialization on Bombacaceae is more likely apomorphic. If so, it is unlikely that *Loxolomia*, *Grammopelta*, and *Almeidaia* will be found to feed on Bombacaceae. Oxytenidae are specialists on Rubiaceae (Jordan 1924, Nentwig 1985), whereas Ceratocampinae utilize several plant groups, not including Bombacaceae (d'Araújo e Silva et al. 1968, Lemaire 1988). The families Myristicaceae, Sapotaceae, Santalaceae, Bombacaceae, Rubiaceae, and Lythraceae are all in different orders (Lawrence 1951).

Analysis of Characters

Characters used in the present cladistic analysis are detailed below. In each case, out-group comparison was used as far as possible to de-

termine character polarity in Arsenurinae. Under each one, my reasons are given to reduce chances of misinterpretation of my methods. The results are tabulated in Table 2. Letters without a prime mark represent the plesiomorphic condition, letters with one prime mark the apomorphic condition, and with two prime marks the most apomorphic condition in a transformation series.

- A. Antennal cones. A = simple; A' = multiple. The multiple cones are the apomorphic condition according to Michener (1952). This is evidently a character that is easily reversed and thus not very useful in the present phylogenetic analysis.
- B. Antennae in male. B = quadripectinate; B' = quadridentate; B'' = simple. Longer projections, the longest ones called rami, are plesiomorphic within the Saturniidae and most other Bombycoidea.
- C. Antennae in female. C = quadripectinate; C' = quadridentate; C'' = simple. Presumed polarity is based on same reasoning as in character B above.
- D. Shape of antennal rami. D = flattened, straight rami; D' = longer, curved rami. Out-group comparison is based on other saturniid groups, since the groundplan bombycoid antenna is bipectinate and therefore of no relevance here (R. Oberprieler pers. comm.).
- E. Forewing apex and outer margin. E = smooth edge; E' = scalloped. The undulating edges of wings as seen in the few genera of Arsenurinae are very rare in Saturniidae and all Bombycoidea in general but are common in several groups of Geometridae (not considered here to be an out-group). Scalloped margins occur in the hindwings but not the forewings of the long-tailed *Antistathmoptera* Tams (Saturniinae: Pseudapheliini), a genus of African moths superficially resembling *Copiopteryx*. Scalloped outer margins are regarded as apomorphic in Arsenurinae.
- F. Hindwing with tail. F = untailed (normal); F' = short tail; F'' = long tail. This character is known to occur in unrelated saturniid groups (Peigler 1989:104).
- G. Uncus. G = simple; G' = bifid. Although both situations occur in several saturniid subfamilies, it appears that the simple condition is plesiomorphic within Arsenurinae because it exists in *Almeidaia* and *Grammopelta*, genera that Michener (1952) and Lemaire (1980) considered to be the most primitive arsenurines based on other evidence.
- H. Fenestrae in wings. H = absent; H' = present. These are absent in all Ceratocampinae except *Neocarnegia* Draudt (Lemaire 1988) and rare in the other bombycoid families, so their presence in Arsenurinae is considered to be apomorphic.
- I. Labial palpi. I = three-segmented, with large third segment; I' = three-segmented, with reduced third segment; I'' = two-segmented. Michener (1952:356) and Lemaire (1988:12) indicated that the three-segmented condition is plesiomorphic. The condition varies between one and three segments in Ceratocampinae, Hemileucinae, and Saturniinae.
- J. Radial veins in forewing. J = four-branched; J' = three-branched or four-branched (both cases exist within a single genus); J'' = three-branched. Reduction in branches is apomorphic based on out-group comparison.
- K. Prothoracic tibial spur. K = present; K' = absent. The presence of this prominent spur in *Almeidaia* is considered plesiomorphic on the basis of the outgroup comparison (e.g., *Eacles*).
- L. Metathoracic tibial spurs. L = present; L' = absent. A pair of spurs is present in certain Oxytenidae (Jordan 1924, pl. 12), Eupterotidae, Lasiocampidae, Anthelidae, Sphingidae, and Bombycidae (Common 1990). Loss of these is considered to be apomorphic. It is not clear if those present in the Arsenurinae are homologous to those present in other groups. Hence the interpretation of their presence as plesiomorphic is not certain.
- M. Lateral spiny protuberances on aedeagus. M = absent; M' = present but weak; M'' = present and prominent. Although comparable structures occur in certain species of *Eacles* (Ceratocampinae) (Lemaire 1988) and Cercophanidae (Jordan 1924, pl. 21), the occurrence of these in Arsenurinae is considered apomorphic. These are absent

in most species of all out-groups. Their occasional presence in diverse groups is clearly the result of homoplasy.

- N. Size of prothoracic dorsal scoli in 1st instar larva. N = large; N' = medium; N'' = tiny. The large condition is plesiomorphic. Large scoli occur in Ceratocampinae, Agliinae, and Hemileucinae (Kuroko 1976, Packard 1905).
- O. Setae of prothoracic dorsal scoli in 1st instar larva. O = two setae; O' = three setae; O'' = 5 or 10 setae. The condition of two setae is apparently the plesiomorphic state because it occurs in Ceratocampinae and Hemileucinae. In other groups, such as Bombycidae and Saturniinae, clusters of numerous setae are found in this position (Nässig 1989). There are five setae per scoli in *Caio richardsoni* and ten in *C. championi*.
- P. Shape of prothoracic dorsal scoli in 1st instar larva. P = normal, with setae; P' = flattened apex. Whether the flattened portion is a seta, or the seta is lost and the apex itself is flattened is not clear. Here the flattened apex is regarded as the apomorphic condition. The flattened swollen tips of some Ceratocampinae appear to be very different from this condition and are almost certainly not homologous.
- Q. Size of prothoracic subdorsal scoli in 1st instar larva. Q = large, bifid; Q' = small to tiny. The large and bifid condition is the plesiomorphic one as it occurs in Ceratocampinae and Agliinae.
- R. Setae of prothoracic subdorsal scoli in 1st instar larva. R = 2 setae; R' = 3 setae. The condition of two setae is normal (plesiomorphic) in Ceratocampinae, Brahmaeidae, and other out-groups. Three species of *Arsenura* examined possess two such setae, whereas these scoli in *A. armida* have none. According to Lordello and Mariconi (1953), two setae are present in *A. xanthopus* (Walker).
- S. Shape of prothoracic subdorsal scoli in 1st instar larva. S = small, bulbous or slightly elongated; S' = elongated and flattened. The long flattened scoli are judged to be apomorphic.
- T. Mesothoracic dorsal scoli in 1st instar larva. T = large, bifid; T' = small, bifid; T'' = tiny, simple. Judging from out-groups such as Ceratocampinae, Brahmaeidae, and Hemileucinae, larger and bifid scoli represent the plesiomorphic condition. In all larvae of Arsenurinae examined, two setae are present on each scoli.
- U. Mesothoracic subdorsal scoli in 1st instar larva. U = bifid; U' = simple. Judging from out-groups, the bifid condition is plesiomorphic. In all larvae of Arsenurinae examined, two setae are present on each scoli.
- V. Bases of dorsal and subdorsal prothoracic scoli. V = not fused; V' = fused. These scoli are relatively large in Ceratocampinae, but the bases are not fused. Fusion occurs in all known arsenurine larvae except in *Arsenura*. In the latter genus, all four scoli may be set within a large prothoracic sclerite, suggesting the beginning of fusion.
- W. Hostplants. W = feeding on plants besides Bombacaceae; W' = specializing on Bombacaceae. This character is included to reinforce the clade of three or four genera that specializes on Bombacaceae.

RESULTS AND DISCUSSION

The two cladistic methods (tabulating synapomorphies and the PAUP analysis) resulted in different hypotheses of the phylogeny as shown in Figs. 19 and 20. Both trees suffer from the lack of data as shown in Table 2, i.e., larvae not known for three genera. The set of data based on adult structure of pinned specimens could be improved by adding characters derived from scanning electron microscopy. Based on the adult and larval characters used, the two cladograms (Figs. 19, 20) represent the most likely hypotheses of the phylogeny of the subfamily. These two phylogenetic trees actually agree in four of the nine branching sequences. The alliance of *Titaeta*, *Dysdaemonia*, *Paradaemonia*,

and *Caio* is not surprising in view of the appearance of the adult moths. The position of *Almeidaia* as the out-group to all others is likewise expected, and agrees with Lemaire's (1980) placement of this genus into a separate tribe. Lemaire (1980 and pers. comm.) said that *Almeidaia* also shares affinities with Ceratocampinae, and that perhaps this genus should be assigned to its own subfamily. It is apparently an ancient relict like we see in *Aglaia*, *Polythysana* Walker, and *Salassa* Moore, genera which Michener (1952) discussed as having mixtures of subfamily characters. The association between *Copiopteryx* and *Rhescyntis* is unexpected because of the superficially very different wing shapes, yet closer examination of the wing patterns of these two genera as compared to other genera suggests that a true alliance exists.

The PAUP analysis found 12 equally parsimonious trees requiring 60 character state changes. None of the 12 trees generated by the analysis agree closely with the one shown in Fig. 19. The majority rule consensus cladogram is shown in Fig. 20. Rohlf's consistency index (CI) for this cladogram was 0.76.

Regarding hostplant preferences (see Table 3), certain hypotheses may now be formulated. Specialization on Bombacaceae is plesiomorphic for the clade *Titaea* + *Dysdaemonia* + *Paradaemonia* + *Caio*. The one record of *Paradaemonia* feeding on Lythraceae indicates an apomorphic change (i.e., secondary loss of feeding specialization on Bombacaceae, indicated by a W in Fig. 19), supported by additional observations that other species of *Paradaemonia* do not accept Bombacaceae in captivity (K. Wolfe pers. comm.). Release from dependence on Bombacaceae could be related to the fact that *Paradaemonia* has three times the number of species as each of the other genera in its clade, and a relatively wide distribution. If we accept Fig. 19, Bombacaceae are secondarily exploited by *Arsenura*, yet Fig. 20 suggests that this character may be plesiomorphic for the clade of *Arsenura* plus the above four genera. More hostplant records are needed, but they are difficult to obtain for most of the species living in the primary rainforest of the tropics.

The Arsenurinae are not rich in species, as compared to many moth groups, and thus appear to be a relict group with comparatively few surviving representatives. Another reason for the low numbers of species could be that these moths do not speciate rapidly. Except for *Arsenura cymonia* (W. Rothschild), the group is limited to low elevations, and speciation in other Saturniidae has apparently been facilitated in montane habitats (C. Lemaire pers. comm.). Michener (1952) considered Arsenurinae to be the most primitive saturniids. The hypothetical ancestor must have been a large species that did not have a genetic capacity for bright wing coloration (shades of yellow, green, pink, and orange),

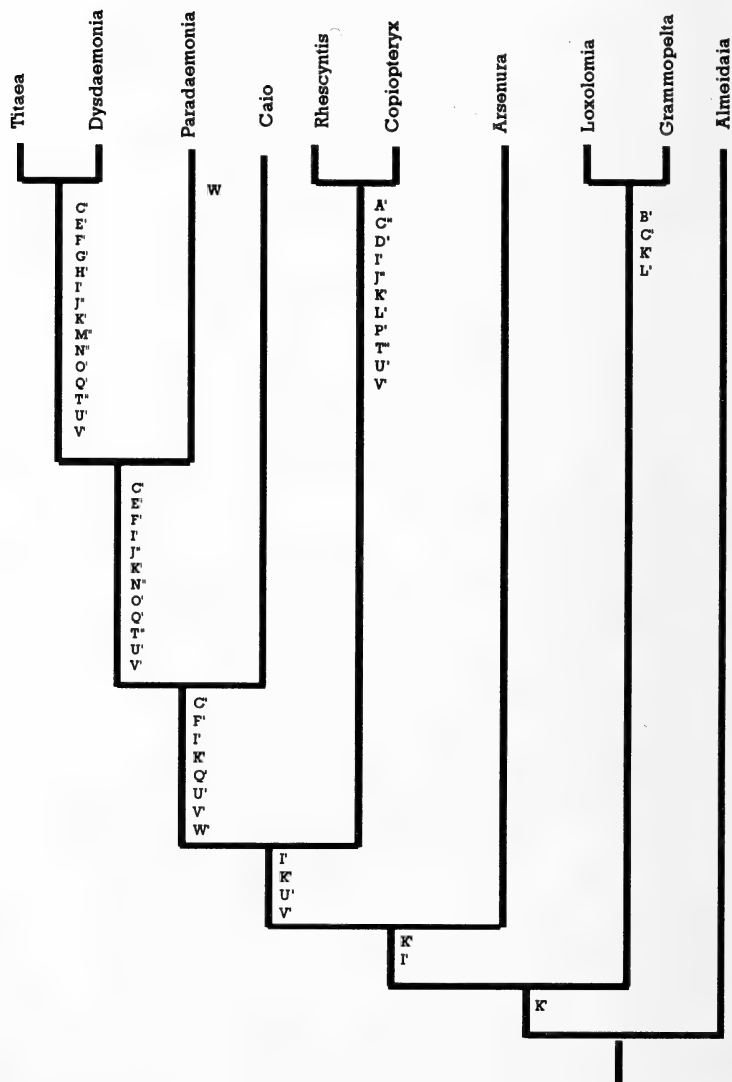


FIG. 19. Cladogram showing proposed relationships of genera of Arsenurinae in which synapomorphies are tabulated.

which is common in other saturniid groups. Most genera in the group have only about five species, and the two genera considered most primitive have only one or two species. It is possible that many lineages have died out, leaving several genera with no individual extant sister-groups. The resulting cladograms yield clades in which some genera are considered to be the sister-group of a large aggregate of genera.

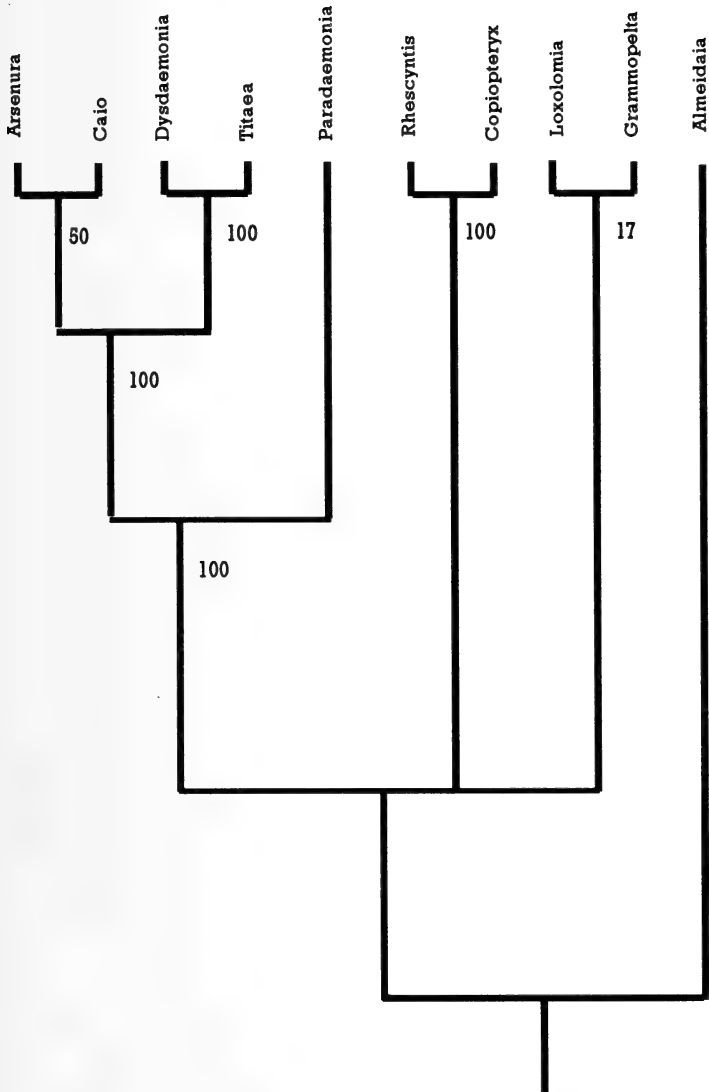


FIG. 20. Majority rule consensus tree showing proposed relationships of genera of Arsenurinae using PAUP analysis. Numbers represent percent of equally parsimonious trees having the respective branching sequence.

Below the generic level, it is clear that *Caio romulus* represents the extant sister-group of the other more northern representatives of its genus. *Caio* was evidently separated into the Mexican (or possibly Guiano-Amazonian) and southern Brazilian components at a time in the past, the former speciating and dispersing (see Halffter 1976, Le-

TABLE 3. Known hostplants of Arsenurinae.

Moth	Hostplant and plant family	References
<i>Arsenura armida</i> (Cramer)	<i>Bombacopsis quinata</i> (Jacq.) Dugand, Bombacaceae; <i>Luehea</i> sp., * Tiliaceae	Janzen (1982)
<i>Arsenura batesi arcaei</i> Druce	<i>Tilia platyphyllos</i> Scop., * Tiliaceae	Brenner & Lampe (1987)
<i>Arsenura polydonta</i> (Jordan)	<i>Chorisia insignis</i> H.B.&K., Bombacaceae	Schreiter (1943)
<i>Arsenura rebeli</i> Gschwandner	<i>Tilia</i> sp., * Tiliaceae	Stone (1991)
<i>Arsenura xanthopus</i> (Walker)	<i>Urena lobata</i> L., Malvaceae	Packard (1914)
	<i>Luehea divaricata</i> Mart., <i>L. grandiflora</i> Mart., <i>L. oerophylla</i> Mart., <i>L. paniculata</i> Mart., Tiliaceae	Lordello & Mariconi 1953
<i>Arsenura</i> sp. (Costa Rica)	<i>Curatella americana</i> L., Dilleniaceae	K. L. Wolfe (pers. comm.)
<i>Arsenura</i> spp. (Brazil)	<i>Anona</i> sp., <i>Rollinia longifolia</i> A.St.Hil., Anonaceae; <i>Ceiba pentandra</i> (L.) Gaertn., <i>Chorisia speciosa</i> St.Hil., Bombacaceae; <i>Luehea divaricata</i> Mart., Tiliaceae; <i>Sterculia excelsa</i> Mart., <i>Theobroma cacao</i> L., Guazuma ulmifolia Lam., Sterculiaceae; <i>Myrsine umbellata</i> Mart., Myrsinaceae; H.B.&K., Euphorbiaceae; <i>Vernonia cinerea</i> Less. (=diffusa), Compositae; <i>Tibouchina</i> sp., Melastomataceae	d'Araújo e Silva et al. (1968)
<i>Cato championi</i> (Druce)	<i>Bombacopsis quinata</i> (Jacq.) Dugand, Bombacaceae <i>Tilia silvestris</i> Desfontaines, * Tiliaceae	Janzen (1982) C. Lemaire (pers. comm.)
<i>Cato richardsoni</i> (Druce)	<i>Chorisia</i> sp., * <i>Ceiba acuminata</i> Rose, Bombacaceae	Stone (1991)
<i>Dysdaemonia boreas</i> (Cramer)	<i>Ceiba pentandra</i> (L.) Gaertn., Bombacaceae <i>Chorisia speciosa</i> St.Hil., Bombacaceae	D. H. Janzen (pers. comm.) Dias (1978)
<i>Dysdaemonia fosteri</i> W. Rothschild	<i>Chorisia insignis</i> H.B.&K., Bombacaceae	Schreiter (1925)
<i>Titaea tamerlan</i> (Maassen)	<i>Chorisia</i> sp., Bombacaceae <i>Bombacopsis quinata</i> (Jacq.) Dugand, Bombacaceae <i>Tilia platyphyllos</i> Scop., * Tiliaceae	Travassos (1946) Janzen (1982) Stone (1991)
<i>Paradaemonia pluto</i> (Westwood)	<i>Cuphea carthagenensis</i> (Jacq.) Macbride (=balsamonea), Lythraceae	d'Araújo e Silva et al. (1968)
<i>Rhescynitis pseudomartii</i> Lemaire	<i>Virola biculhyba</i> (Schott.) Warb., Myristicaceae	Travassos & d'Almeida (1937)

TABLE 3. Continued.

Moth	Hostplant and plant family	References
<i>Rhescyntis hippodamia norax</i> Druce	<i>Viola quatemalensis</i> (Hemsl.) Warb. probably, Myrtaceae	Vázquez (1965)
<i>Copiopteryx semiramis</i> (Cramer)	<i>Lucuma caimito</i> Roem., Sapotaceae <i>Manilkara chicle</i> (Pittier) Gilly, Sapotaceae	Travassos (1946) Janzen (1982)
<i>Copiopteryx semiramis phoenix</i> (Deyrolle)	<i>Acanthosyris spinescens</i> (Mart. & Eichl.) Griseb., Santalaceae	d'Araújo e Silva et al. (1968)
<i>Copiopteryx sonthonnaxi</i> André	<i>Mimusops</i> sp., Sapotaceae	d'Araújo e Silva et al. (1968)

* Hostplant in captivity.

maire 1977). The same north vs. south vicariance appears to apply to the two groupings within *Copiopteryx* as defined by Lemaire (1980). Whether the divergent wing pattern and coloration of *Titaea orsinome* is the result of phylogenetic divergence, or is an ecological adaptation to the plateaus of central Brazil is unknown, but I suspect the latter to be the case. The other genera are quite homogenous in the wing fascia among their species. Possible interpretations of why the genus *Arsenura* is much more species-rich include the following. It is able to speciate more rapidly, or is more adaptable and therefore declining less rapidly. The proposed hypotheses of the phylogeny do not support the idea that this group has more species because it is an older lineage.

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LIFE HISTORY OF *ELYMNIAS AGONDAS GLAUCOPIS*
(NYMPHALIDAE: SATYRINAE), A PEST OF OIL
PALM IN PAPUA NEW GUINEA

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ABSTRACT. The early stages of *Elymnias agondas glaucopsis* Staudinger in Papua New Guinea are described and illustrated. This species has transferred from native palms to introduced species, such as the oil palm (*Elaeis guineensis* Jacq.), and has become a minor pest. The average length of life cycle on palms and bananas was 48 days ($n = 9$) at an ambient temperature of 27°C. Two species of *Brachymeria* (Hymenoptera: Chalcididae) were recorded as parasitoids of the pupae.

Additional key words: *Elaeis guineensis*, parasitism, natural enemies.

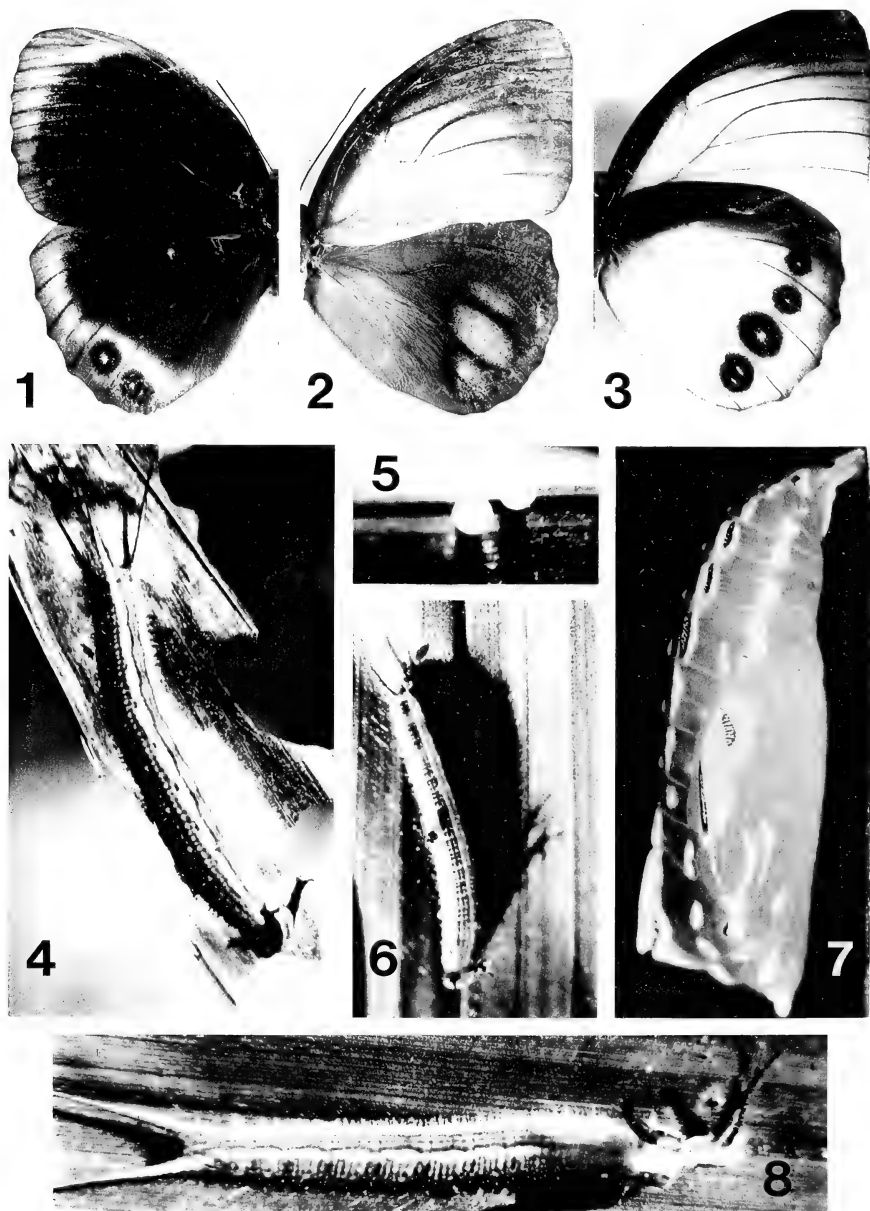
Elymnias agondas glaucopsis Staudinger (Nymphalidae) (Figs. 1–3) is a medium-sized nymphalid butterfly that occurs in northeastern Papua New Guinea. Throughout its geographical range, the larvae utilize native palms as larval host plants. Following the introduction of the oil palm (*Elaeis guineensis* Jacq., Palmae) to Papua New Guinea, *E. agondas glaucopsis* began using this species as well. As a consequence, *E. agondas glaucopsis* currently is considered a minor pest of oil palm in Papua New Guinea. This story closely parallels one in Malaysia where *Elymnias hypermnestra* Fruhstorfer transferred from native species [e.g., *Areca* and *Cyrtostachys* (both Palmae) and *Bambusa* (Graminae)] to oil palm and coconut (*Cocos nucifera* L., Palmae) (Lepesme 1947).

The early stages of *Elymnias agondas australiana* Fruhstorfer were described briefly by Wood (1984). In this paper I describe the early stages of *E. agondas glaucopsis* for the first time and report color differences between the larvae of these two subspecies. I also report on larval survival on various food plants and identify predators and parasitoids of *E. agondas glaucopsis*.

MATERIALS AND METHODS

I collected larvae, pupae, and females of *E. agondas glaucopsis* at the National Botanic Gardens in Lae, Morobe Province, Papua New Guinea, in July 1986, and at the Papua New Guinea University of Technology, 10 km away from the Botanic Gardens, from July 1986 to June 1987. From May to July 1988, adults were netted in flight or trapped at fermenting banana bait at the Papua New Guinea University of Technology. Larvae and pupae discovered in the field were reared in the

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FIGS. 1-8. *Elymnias agondas glaucopsis*. 1, Upperside of male; 2, Upperside of female; 3, Underside of female; 4, Third instar larvae; 5, Eggs; 6, Second instar larva; 7, Pupa; 8, Fifth instar larva eating shed exuvium.

laboratory or sleeved on foodplants outdoors to obtain parasitoids and adult butterflies. Reared and field collected females were used to obtain eggs to assess larval survival on various hosts, and to obtain eggs, larvae, and pupae for descriptions of the early stages.

During the 1988 season, the rearing protocol was as follows. As first instars hatched, they were transferred to cut leaves in glass jars. Larvae were offered one of the following: betel-nut (*Areca catechu* L.), coconut (*Cocos nucifera*, Palmae), cycad (*Cycas circinalis* L., Cycadales), or banana (*Musa acuminata* Colla and *M. balbisiana* Colla, Musaceae). Not more than six larvae were confined per jar.

Parasitoids that emerged from field collected larvae and pupae, and predators of larvae observed on sleeved foodplants, were recorded and sent to the Commonwealth Agricultural Bureau International Institute of Entomology, London, for identification. Specimens of the larvae and pupae of *E. agondas glaucopis* are deposited in the Natural History Museum, London (voucher nos. BMNH ES 3238–3244).

Descriptions of the early stages are composite, based on all eggs, larvae, and pupae either collected in the field or obtained via reared females. Because larval size varied with age, nutritional state, and hydration, a range is provided for all measurements in the descriptions below. Where possible, healthy larvae were used for the descriptions. Measurements of length of larvae do not include the anal processes.

RESULTS

Early Stages

Egg (Fig. 5). Oblate spheroid, ca. 1.5 mm in diameter; pearl white when laid; chorion darkening slightly before hatching; surface smooth when observed with hand lens ($\times 10$). Laid singly or occasionally in pairs on upper surface, or more commonly, on under surface of leaf.

First instar. Newly hatched larva whitish, with shiny, light brown head. Head armed with ten stout black spines tipped with white. Paired dorso-lateral posterior spines subsequently develop into horns. Head and body covered with white hairs terminating in glandular tip. Anal segment produced dorsally into two green processes, each 1.0 mm in length and bearing a white-tipped black spine. Length of larvae increases from about 4.0 mm ($n = 45$) to 6.5 mm ($n = 35$).

Second instar (Fig. 6). Head with two dark brown palmate horns, each bearing five black spines tipped with white; two dark brown stripes extend across frons, appearing continuous with horns. Two dark brown spines on either side of the head and four black warts posterior and ventral to horns. Body green, paler below; two longitudinal yellow lines outlining dorsal vessel, which appears darker green. Paired thick yellow

lines dorso-laterally and laterally; faint yellow line below spiracles. Spiracles yellow. Anal processes black, terminating in spines with white distal bulbs; processes united at base by black bar. Short white hairs arise from raised tubercles. Length of larvae increases from about 7.5 mm ($n = 4$) to 12.5 mm ($n = 2$).

Third instar (Fig. 4). Head with four pairs of upward-curving light brown spines laterally. Body with yellow dorso-lateral stripes mixed with orange and blue-green; blue-green lacking on segments 11 and 12. Dorso-lateral lines running into pink anal processes tipped with black on segments 11 and 12. Anal processes yellow in *E. agondas australiana* (Wood 1984). Length of larvae increases from about 15 mm ($n = 4$) to 22 mm ($n = 1$).

Fourth instar. Head with irregular white creamy patches and black spines from light brown pedicels. Base of horns knobby. Body with two thick dorso-lateral longitudinal lines subdivided into six yellow compartments on each segment, second to fourth compartments with orange patches (brightest in third) surrounding central hair. Fifth compartment with elongate blue-green spot. Spiracles brown, linked by wavy yellow lines. Anal processes pink, 6 mm long. Length of larvae increases from about 24 mm ($n = 4$) to 29 mm ($n = 4$).

Fifth instar (Fig. 8). Head about 4.3 mm in width ($n = 6$; measured from shed skins), with horns and accompanying spines black; lateral spines light brown tipped with black. White spots near antero-lateral stripes and jaws, as reported for *E. agondas australiana* (Wood 1984). Prothorax with two dorsal yellow spots. Anal processes pink; yellow in *E. agondas australiana* (Wood 1984). Spiracles orange-yellow. Length of larvae increases from about 31 mm ($n = 1$) to 40 mm ($n = 1$).

Pupa (Fig. 7). Apple green, becoming paler with age. Head with two anteriorly directed yellow horns marked with black; horns in *E. agondas australiana* black and white (Wood 1984). Dorsal mid-line centered with pink, interrupted, running from small swelling on prothorax to cremaster. Dorsal line turns 90° at posterior end of mesothorax. Wing cases marked with yellow, pink, and black concentric circles and lenticular patches. Costa of forewing outlined with yellow and pink. Cremaster yellow with three black dots. Body is bent so that it is held parallel to substrate. Length 22–27 mm, width 8 mm ($n = 5$).

Eggs held at 27°C hatched in five to seven days. Each larval stage, from first through fourth instar, ended with a day or two of inactivity as a pharate larva. First and fourth instar typically lasted about 5 days; second and third instar typically lasted about 6 days. A day or two was spent as a pharate pupa, indicated by a swollen and yellowish prothorax. The total length of the life cycle varied between 44 days (on narrow leaved *Ptychosperma* sp.) and 51 days (on banana—*Musa acuminata*

TABLE 1. Foodplants of *Elymnias agondas glaucopsis* in Papua New Guinea (PNG). All supported complete development from first instar, where noted.

Species	Area native to	Evidence of potential use by <i>E. agondas</i>
<i>Brassiophoenix schumanii</i>	PNG	7 larvae and 1 pupa found in field.
<i>Caryota rumphiana</i>	PNG	2 larvae and 1 pupa found in field.
<i>Chrysalidocarpus lutescens</i>	Madagascar	1 egg laid in field—completed development.
<i>Cocos nucifera</i>	PNG	P. Clark (pers. comm.). 1 larva completed development.
<i>Cycas circinalis</i>	PNG	1 pupa found in field.
<i>Elaeis guineensis</i>	W. Africa	R. Prior (pers. comm.). 1 larva completed development.
<i>Musa acuminata</i> & <i>balbisiana</i>	PNG	3 larvae completed development.
<i>Ptychosperma</i> spp.	PNG	5 larvae and 2 pupae found in field. 2 larvae completed development.
<i>Roystonea regia</i>	Cuba	1 larva and 2 pupae found in field.

and *M. balbisiana*). These findings agree with those of Wood (1984), who reported 5 days for the egg stage and 49 days for the total life cycle of *E. agondas australiana*.

Foodplants

Larvae of *E. agondas glaucopsis* completed development on a variety of palms, both native and introduced (Table 1). Larvae and pupae were collected in the wild from *B. schumanii*, *C. rumphiana*, narrow leaved *Ptychosperma* sp., and *R. regia*. A single egg was collected from *C. lutescens*, and a parasitized pupae was found on *C. circinalis*. In the Higaturu oil palm plantations in the Northern Province of Papua New Guinea, *Elymnias agondas glaucopsis* is abundant, utilizing oil palm as the larval hostplant (R. Prior pers. comm.). It also utilized *C. nucifera* in the wild (P. Clark pers. comm.). In captivity, *E. agondas glaucopsis* successfully developed on *Chrysalidocarpus lutescens*. Wood (1984) obtained oviposition of *E. agondas australiana* on *Calamus caryotoides*.

First instar larvae of *E. agondas glaucopsis* fed on all plant species offered: *Areca catechu*, *Areca* sp., *Cocos nucifera*, *Cycas circinnalis*, *Musa acuminata*, and *M. balbisiana*. However, all larvae reared confined with *Areca catechu* (n = 25), *Areca* sp. (n = 2), and *Cycas* (n = 6) died before completing development. Of 20 first instar larvae confined with *Areca catechu* and two confined with *Areca* sp., 16 died before the next ecdysis. Of five fifth instar larvae transferred to *Areca catechu*, only one resulted in a pupa, and it was deformed. Some individuals had deformities following ecdysis to the fourth instar, particularly of the horns and anal processes. Of 14 larvae confined with

Cocos nucifera, only one reached adulthood; two larvae reared on coconut had shortened anal processes. Of four larvae confined with banana leaves (*Musa acuminata* and *M. balbisiana*) throughout, three survived to adulthood. Of seven larvae transferred to cut coconut and banana leaves from a defoliated potted oil palm, two completed development on coconut and two on banana.

Natural Enemies

Of twelve pupae collected in the wild, four (33%) were parasitized by *Brachymeria* nr. *jambolana* Gahan and one (8%) by *Brachymeria* nr. *lasus* (Walker) (Hymenoptera: Chalcidoidea). Larvae sleeved outdoors in 1988 were attacked by immature *Pristhesancus femoralis* Horvath (Heteroptera: Reduviidae) and *Montrouzeriellus melacanthus* (Boisduval) (Heteroptera: Pentatomidae). Debris and spider mites (Acarina: Tetranychidae) were observed sticking to the glandular hairs of fourth and fifth instar larvae. The hairs may function as a defense against some predators and parasitoids.

Both larvae and adults were preyed upon by house geckos (*Hemidactylus frenatus* Dumeril and Bibron; Sauria: Gekkonidae). Predation upon adults may be reduced owing to mimicry. Female *E. agondas glaucopis* are believed to be Batesian mimics of unpalatable *Taenaris* species (Nymphalidae: Amathusiinae) and *Euploea* species (Nymphalidae: Danainae) (Fruhstorfer 1913, Parsons 1984). Within the study area, *Taenaris catops* Westwood ($n = 2$) were observed imbibing sap exuded from the trunk of a damaged cycad. This behavior is similar to the pharmacophagy exhibited by adult Danainae (Parsons 1984) and may confer a degree of unpalatability to this species. *Euploea* species are believed to sequester toxic glycosides and alkaloids from their hosts. Male *E. agondas glaucopis* may be Batesian mimics of *Taenaris onolaus* Kirsch. The latter is assumed to be unpalatable to predators owing to its foodplant, *Cycas circinalis*, which is known to be toxic to livestock (Hooper 1978, Henty 1980). It is interesting to note that adult *Taenaris onolaus* were ignored by geckos under situations similar to those where *E. agondas* were eaten.

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GENERAL NOTES

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A NATURAL HYBRID BETWEEN *CALLOPHRYS* (*CALLOPHRYS*) *SHERIDANII* AND *C. (INCISALIA) AUGUSTINUS* (LYCAENIDAE)

Additional key words: male genitalia, valvae, *Mitoura*, homology.

Scudder (1872) described *Incisalia* and noted its similarity to *Callophrys* Hübner. Since then, *Incisalia* and *Callophrys* have been treated as subgenera (Ziegler 1960, Clench 1961) or closely related genera (Miller & Brown 1981). The presumed hybrid that we report here is remarkable, whether it is considered intergeneric or intersubgeneric, and further highlights the genetic similarity of *Incisalia* and *Callophrys*.

An apparent male hybrid (Fig. 1) between *C. sheridanii* (Edwards) and *C. augustinus* (Westwood) was captured by the senior author on a dry slope (2950 m) below Cottonwood Point, 6.5 southwest of Hot Sulphur Springs, Grand Co., Colorado, USA, on 28 May 1990. It was flying among individuals of *C. augustinus* in an area with low evergreen shrubs and *Arctostaphylos uva-ursi* L. (Ericaceae), which is the local larval foodplant for *C. augustinus*. Individuals of *C. sheridanii* were common about 100 m away in an area

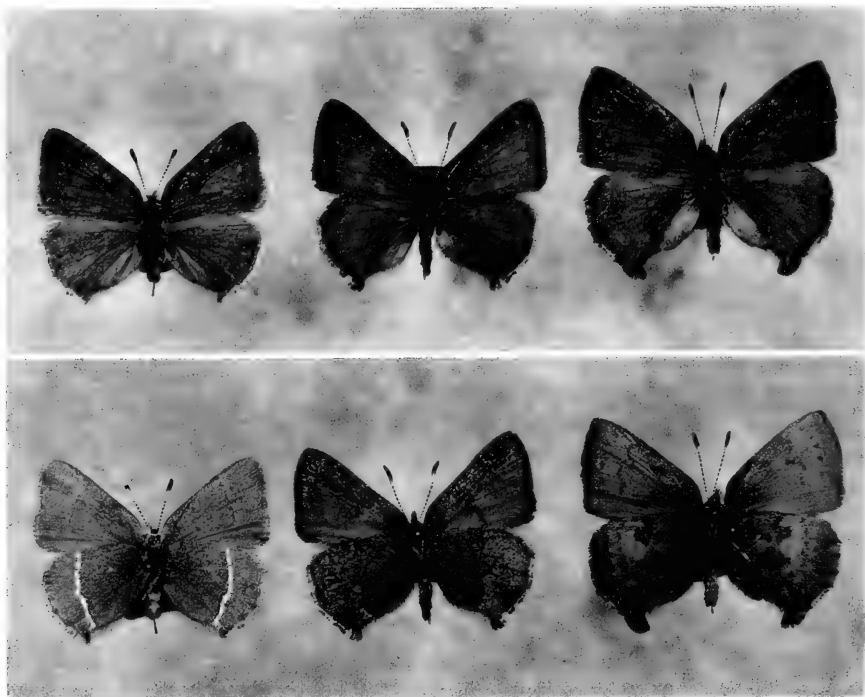


FIG. 1. Dorsal (top row) and ventral aspect of butterflies from Cottonwood Point, Colorado. From left to right, *C. sheridanii*, the presumed hybrid, and *C. augustinus*. Photograph by James Scott.

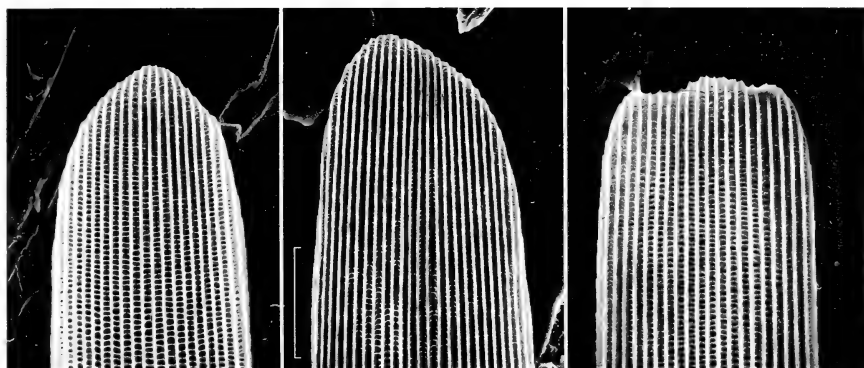


FIG. 2. Distal end of dorsal forewing androconia. From left to right, *C. sheridanii*, the presumed hybrid, and *C. augustinus*. Scale 15 μ m.

dominated by *Artemisia tridentata* Nuttall (Asteraceae) and with occasional stands of *Eriogonum umbellatum* Nuttall (Polygonaceae), which is the local larval foodplant for *C. sheridanii*. Thus, adults of the presumed "parent" species of the hybrid are common in the same general vicinity at the same time of year.

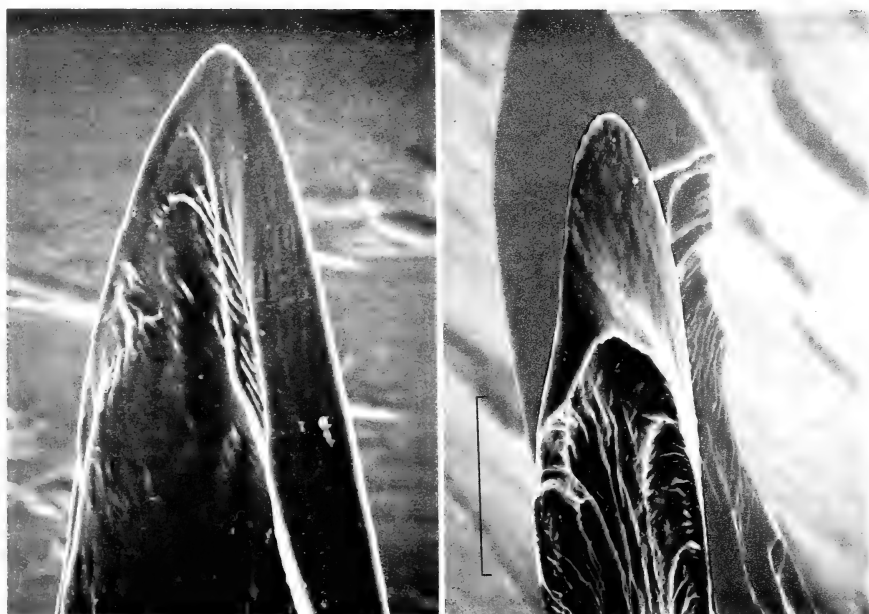


FIG. 3. Thickened tips of the left valva in the male genitalia (ventral aspect). From left to right, *C. sheridanii* and *C. augustinus*. Scale 38 μ m.

TABLE 1. Characters in *C. sheridanii*, the presumed hybrid, and *C. augustinus* from Cottonwood Point, Colorado. Genitalic measurements are \pm one standard deviation with sample size of 9. Abbreviations: V, ventral; D, dorsal; Pm, postmedian; HW, hindwing; FW, forewing.

Character	<i>C. sheridanii</i>	Hybrid	<i>C. augustinus</i>
	Wing and head characters		
1. V coloration	green & gray	green & brown	red-brown
2. Hindwing shape	rounded	intermediate	angular
3. Anal lobe	short	intermediate	long
4. V Pm line shape	nearly straight	slightly jagged	jagged
5. V Pm line position	submarginal	postmedian	postbasal
6. VHW Pm line color	white	white & brown	brown
7. Wing fringe color	white, some gray	gray, some white	gray
8. Androconia	rounded	rounded	dentate
9. Scales around eye	white	brown, some white	brown, some white
	Genitalic characters		
1. Valva thickening	tips & inner margin	tips & part (?) of inner margin	tips
2. Penis length (mm)	3.62 ± 0.196	3.44	3.04 ± 0.117
3. Valvae length (mm)	1.31 ± 0.052	1.33	1.20 ± 0.062
4. Saccus length (mm)	0.64 ± 0.050	0.52	0.47 ± 0.049

Clench (1961) noted three differences between *Incisalia* and *Callophrys*. The ventral ground color of *Callophrys* is green and that of *Incisalia* brown; the hybrid has a mixture of brown and green (Table 1). Androconia of *Callophrys* are rounded whereas those of *I. augustinus* are "dentate" (Fig. 2). Androconia of the hybrid are rounded like those in *Callophrys* (Fig. 2). Tips of the valvae in the male genitalia are thickened in *Incisalia* but not in *Callophrys* (Clench 1961). However, we found that the tips are thickened in both taxa (Fig. 3), although less prominently in *C. sheridanii*, where the thickening continues along the inner margin of the valves, as it does in *Mitoura* (Robbins unpubl. data). We did not photograph the valvae of the hybrid because preparation for the scanning electron microscope would have destroyed the genitalia. However, the thickened tips of the valvae, viewed with a light microscope, appeared to be intermediate, but more similar to *C. sheridanii*.

We scored other differences between Cottonwood Point individuals of *C. augustinus* and *C. sheridanii* to test further the hypothesis that this individual is an interspecific hybrid. We noted 6 other differences in wing pattern (Table 1), and in each case the hybrid was intermediate. Many of these characters can be seen in Fig. 1. Color of scales surrounding the hybrid's eye was the same as that in *C. augustinus* (Table 1). We also compared lengths of structures in the male genitalia (Table 1) using *t*-tests. The penis of the hybrid was significantly longer than that of *C. augustinus* ($t_s = 3.243$, $df = 8$, $P < 0.05$), but statistically indistinguishable from that of *C. sheridanii* ($t_s = -0.871$, $df = 8$, $P > 0.4$). The valvae of the hybrid were marginally longer than those of *C. augustinus* ($t_s = -1.989$, $df = 8$, $0.1 > P > 0.05$), but indistinguishable from those of *C. sheridanii* ($t_s = 0.365$, $df = 8$, $P > 0.5$). The saccus of the hybrid was marginally longer than that of *C. sheridanii* ($t_s = -2.277$, $df = 8$, $0.1 > P > 0.05$) and indistinguishable from that of *C. augustinus* ($t_s = 0.0968$, $df = 8$, $0.4 > P > 0.2$). The presumed hybrid specimen is deposited in the National Museum of Natural History, Smithsonian Institution.

Interspecific hybridization is prevented in nature by pre-mating isolating mechanisms and by differences in genetic regulation that cause abnormal development (Remington 1958, Oliver 1979). For these reasons, interspecific hybrids are uncommon in nature. Hand-mating techniques (Platt 1969 and included references) and hormonal treatments (Clarke & Willig 1977) are often necessary to produce such hybrids in the laboratory. Although interspecific hybrids occur consistently in some groups, such as *Limenitis* F., only one hypothesized New World hairstreak (Eumaeini) hybrid has been reported previously (Robbins & Venables 1991). The hybrid described above is thus remarkable.

The biological significance of the presumed hybrid between *C. augustinus* and *C. sheridanii* is that it provides information on homology. For example, position of the hybrid's ventral hindwing postmedian line is intermediate between those in *Callophrys* and *Incisalia*, indicating that this line is homologous in the two species. If the postmedian lines were not homologous, then both lines would be expected to be expressed in the hybrid. While the presumed hybrid provides no information on phylogeny within *Callophrys* (genetic similarity is a shared primitive trait derived from the last common ancestor), it indicates that *Incisalia* and *Callophrys* are genetically very similar, whether they are considered subgenera or genera.

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FIRST RECORD OF *DARAPSA MYRON* (SPHINGIDAE) FROM THAILAND

Additional key words: hawkmoth, *Polyalthea*, Annonaceae, introductions.

While rearing swallowtail larvae (Papilionidae) from *Polyalthea longifolia* Benth. (Annonaceae) in Banglamphu, Bangkok, Thailand, sphingid larvae were collected inadvertently along with host material, and placed in a polythene bag (12 December 1991). The sealed bag was taken to England, where upon opening revealed two sphingid prepupae. Following successful pupation, two male moths emerged (Fig. 1)—one on 29 December 1991 and the other on 5 January 1992. The specimens were taken to The Natural History Museum, London, England, for identification. The genitalia of one specimen (BM sphingid slide #488) were dissected. They proved to be identical to those of the American species *Darapsa myron* (Cramer). A male from Eagle Lake, Texas, was dissected (BM sphingid slide #489) for comparison, and the identification was confirmed. Both specimens from Bangkok and their pupal cases are deposited in the collection of The Natural History Museum.

During more than five years of field work and research on the Sphingidae of Thailand, we have never encountered *D. myron*. Furthermore, R. D. Kennett, who has been surveying the sphingids of Bangkok for several years, has not recorded this species either. We therefore suspect that *D. myron* has arrived in Thailand recently. The origin of the Bangkok colonists is unclear. Although Sphingidae frequently are bred in North America and Europe by collectors, we are unaware of anyone who is rearing them in Thailand. In addition, *D. myron* is unlikely to warrant such attention because it is not a particularly attractive species. We therefore conclude that *D. myron* was introduced into Thailand inadvertently. A possible source of introduction may have been a gravid female that was captured in the cargo hold of an aircraft leaving the United States and released upon arrival at Don Muang Airport in Bangkok. Alternatively, eggs or larvae may have been present on plant material imported from the United States that subsequently was transported to a flower market near Banglamphu. Regardless of its means of arrival, unless we accept the unlikely hypothesis that the larvae were discovered only one generation following the species' arrival, we conclude that *D. myron* is breeding successfully in Bangkok.

In North America, *D. myron* feeds on Vitaceae and Caprifoliaceae (Hodges 1971).

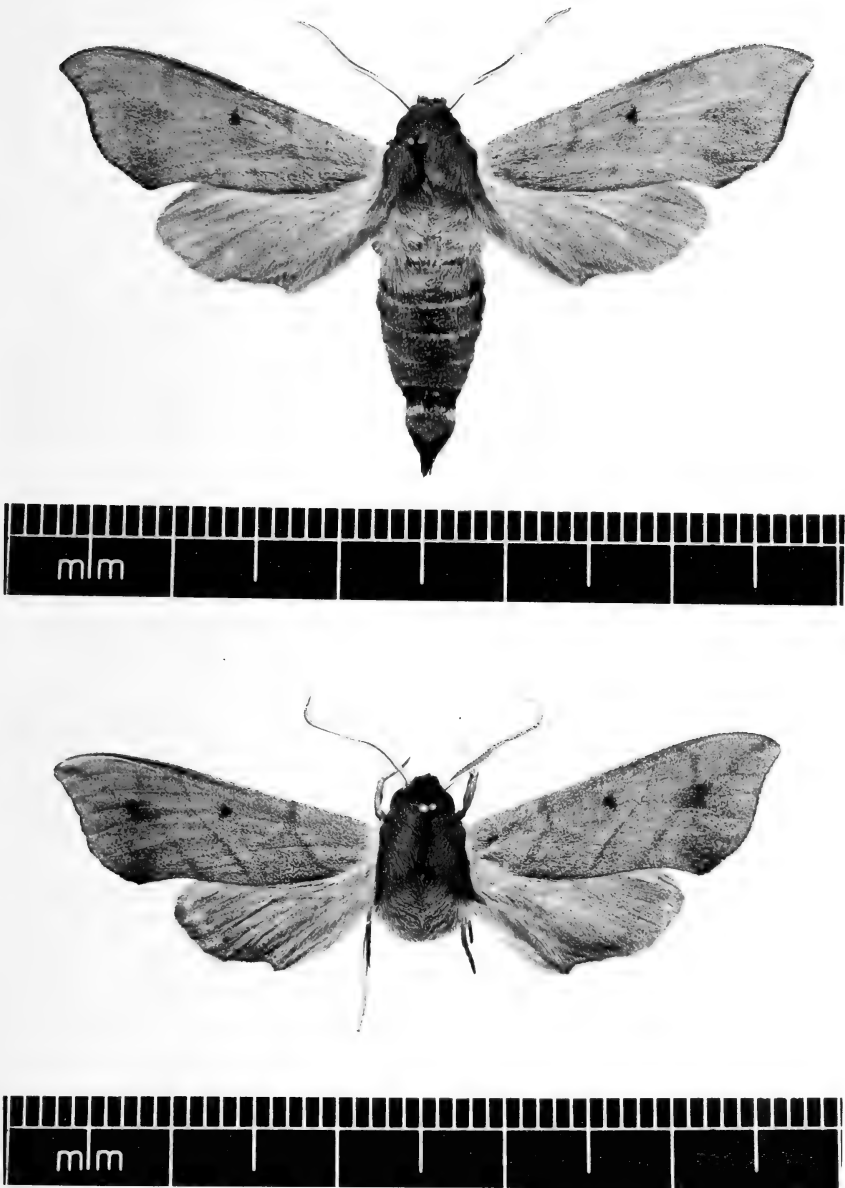


FIG. 1. Males of *Darapsa myron* from Bangkok.

Annonaceae are not closely related to either of these families, and therefore, *Polyalthia* is an unusual hostplant record. The two moths are dwarfs, being only two-thirds the size of typical specimens. This may be because *Polyalthia* is a suboptimal larval food plant, or because of the unnatural rearing conditions. Although smaller than typical *D. myron*,

the genitalia of the dissected male are identical to those of the Texas male and probably were capable of normal function.

What is the fate of *D. myron* in Thailand? *Polyalthea* was introduced to Thailand from India. It is grown widely as an ornamental in most towns and cities and along many major highways throughout Thailand. If *D. myron* can develop successfully on this host, there is no reason why the moth could not expand its range from Bangkok to encompass most of Thailand and perhaps beyond. Alternatively, *D. myron* may encounter native Vitaceae or Caprifoliaceae that it may be capable of using as a larval host plant.

We thank H. Taylor, Photographic Unit, NHML, for providing the photographs of *D. myron*.

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LONG-RANGE DISPERSAL AND FAUNAL RESPONSIVENESS TO CLIMATIC CHANGE: A NOTE ON THE IMPORTANCE OF EXTRALIMITAL RECORDS

Additional key words: distribution, *Nathalis iole*, *Phoebis sennae*, drought, El Niño.

On 27 June 1992 I collected a female *Nathalis iole* (Bdv.) (Pieridae) at Donner Pass, Nevada Co., California (2100 m). This was the second *N. iole* I had seen in the northern Sierra Nevada in 21 years of almost constant field work. Such extralimital records—the proverbial “strays” far from their normal ranges—can be found in almost all regional faunas. Although memorable to the individual collector, such records are typically not considered important. I would argue that in the context of global climatic change, such records are *biologically* important.

Because of its Mediterranean climate, California precipitation is tallied by “water year” (July 1–June 30), not calendar year. West of the Sierra-Cascade axis most of the precipitation falls from November to April. Mediterranean climates are geologically young and inherently unstable, with very high variance in precipitation on several time scales (Axelrod 1973, Major 1977, Fritts and Gordon 1980). 1992 was the sixth year of “drought” (as recognized by state and Federal agencies concerned with water management) in California. Although the intensity of “drought” and the definition of the term are subject to interpretation, biological indicators of drought stress were abundant. Levels of conifer morbidity and mortality in the Sierra Nevada reached 30–50% by late 1992, with firs (*Abies*, Pinaceae) particularly affected. Even with dramatically increased precipitation in winter 1992–93, the composition of Sierran vegetation already had been altered both qualitatively and quantitatively in ways which will persist for decades. We know from palynological, dendrochronological, and pedological data that such climatically-induced perturbations have occurred repeatedly since the end of the Pleistocene throughout the mid-latitudes of the Northern Hemisphere, including the Sierra Nevada (R. Byrne pers. comm.). These have resulted in reconfiguration of the species mixes defining “communities,” as well as the altitudinal distributions of species and species assemblages.

The peculiar weather in the Sierra Nevada in 1992 constituted not only an exacerbation of the "drought" but a remarkable simulation of the projected impact in the Sierra of systematic global "greenhouse" warming (Botkin et al. 1991). In this scenario snowpacks will be lighter and will melt very rapidly roughly a month earlier than now (at 2000 m), resulting in a nearly instantaneous transition from winter to early summer conditions. May 1992 temperatures at Donner Pass were near to slightly above historic June norms; snow was entirely gone by early May. A great many organisms appeared four to six weeks earlier than historic (20 yr) norms, and for many butterflies population densities were remarkably high. Although spring 1992 is probably not a result of global warming (indeed, the combination of El Niño and stratospheric albedo effects from Mount Pinatubo should have canceled out global warming in 1992), it gave a glimpse of what the biotic responses to "greenhouse" regimes might be. Of course, one year's experience does not permit extrapolation to longer-term impacts if such regimes were to be sustained or even intensified over many consecutive years.

1992 was a year of many extralimital records, perhaps one of the best in California. Several of these appear to have resulted from heavy rain in the deserts of southern California and Mexico—rains attributed in this case to El Niño, but also forecast in some global warming scenarios. In addition to the strongest migration of *Vanessa cardui* L. (Nymphalidae) since 1973, population outflow was especially evident in desert Pierids. *Nathalis iole* came north on both sides of the Sierra Nevada. There were several high-altitude records in the western Great Basin (C. Nice pers. comm.). On 28 September a male was taken in the Sacramento Valley (West Sacramento, Yolo Co.) and on 8 October another in the Suisun Marsh (Solano Co.). These are new northern records west of the Sierra.

Phoebis sennae marcellina Cramer (Pieridae) also came north. Between 2 May and 23 May I saw five individuals in the Sierra Nevada between 750 and 1770 m, more than I had seen in northern and central California in the preceding 20 years! I also received a report of a *Eurema mexicana* (Bdv.) (Pieridae) taken in the central Sierra Nevada (J. Ausland pers. comm.).

None of these species is likely to become a breeding resident in the short term. Climatic tolerances and availability of resources should see to that. *N. iole* genuinely feeds only on *Bidens* and certain other (mostly photosensitizing) composites. It might be able to breed on garden marigolds (*Tagetes*). *Phoebis* has no native hosts (caesalpinoid legumes) in northern California, and the few woody *Cassia* in gardens were killed in the December, 1990 freeze. In general, however effective their dispersal, phytophagous insects cannot colonize an area until suitable hosts are established. Nonetheless, the rapid appearance of desert Pierids in northern California after short-term weather anomalies implies that apparent barriers are much leakier than is usually thought.

There are thousands of extralimital records scattered in various journals, but few systematic collations of them (e.g., Kaisila (1962) for Finnish Lepidoptera or Hengeveld (1985) for Dutch Coleoptera). Even a cursory review of such data suggests some general patterns (the incidence of southern species far to the north is much greater than the reverse; high-altitude species descend less often than low-altitude ones ascend; seasonal migrators often transcend their normal limits). If directional climatic shifts ensue, today's extralimital records are probably giving us a foretaste of tomorrow's faunas—or at least of the sequence of colonizations to be expected. It is therefore not only worthwhile but important to publish them, and in particular to collate and interpret them, especially in a context of long-term faunistic monitoring (Goldsmith 1991).

This note was inspired by conversations with Roger Byrne (Geography, UC Berkeley) and Allan Ashworth (Geology, North Dakota State University) during a Quaternary seminar at Berkeley in Fall Semester 1992.

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EFFECT OF TEMPERATURE AND RELATIVE HUMIDITY ON CERTAIN LIFE HISTORY TRAITS IN *ANTHERAEA MYLITTA* (SATURNIIDAE)

Additional key words: climate, tasar silk moth, emergence, seasonal variability.

Antheraea mylitta (Drury), the semi-domesticated tasar silk moth, produces three generations annually under commercial rearing conditions, i.e., July–August (rain), September–October (autumn), and November–December (winter). Eggs for commercial rearings are collected from mated females from the grainage—a specially designed, well ventilated house for storage of tasar silk moth cocoons. Emergence of moths occurs from diapausing pupae immediately before each of the rearing seasons. Diapause in the first generation (rain) lasts up to 15 days; that of the second generation (autumn) lasts up to 20 days; and that of the third generation (winter) lasts nearly 150 days. Life history features such as percent emergence, percent coupling, fecundity, and percent hatching of *A. mylitta* are variable between seasons. Some of this variation appears to be influenced by climatic conditions; Jolly et al. (1974) and Nayak and Dash (1989) have demonstrated the influence of climatological factors on reproduction in *A. mylitta*. Understanding the effect of environmental factors upon these life history parameters is important for the maintenance of an appropriate reservoir of cocoons for commercial silk production. Hence, we conducted this study to determine and quantify the relationship of temperature and relative humidity to moth emergence, coupling success, fecundity, and hatching.

Healthy cocoons of *A. mylitta* were collected at random from the commercial grainages at the State Tasar Research Farm, Durgapur, Orissa, India. The cocoons were collected in 5 replications of 1000 individuals at the beginning of each month throughout the rearing season in 1988. The cocoons of each replication were stored separately in wire mesh cages inside the grainages. Daily emergence of adults, along with their sex and mating activity (coupling) were recorded. After mating, females were allowed to oviposit in cardboard boxes. Fecundity and percent hatching were recorded each month. Ambient temperature and relative humidity inside the grainage were recorded daily. The data were analyzed statistically to identify correlations between environmental factors and percent emergence, percent coupling, fecundity, and percent hatching. Student's *t*-test

TABLE 1. Mean values \pm SD of temperature and relative humidity (RH) and mean \pm SD of monthly percentage of emergence, percentage of coupling, fecundity and percentage of hatching of *A. mylitta* during 1988.

Season	Month	Temperature \pm S.D.	Relative humidity \pm S.D.	% emergence		% coupling	Fecundity (no.)	% hatching
				Male	Female			
Summer	March	32.1 \pm 1.09	70.8 \pm 3.12	0.17 \pm 0.04	0.11 \pm 0.01	15.23 \pm 0.03	177.66 \pm 0.03	74.66 \pm 0.03
	April	29.6 \pm 0.98	81.8 \pm 2.91	0.07 \pm 0.01	0.07 \pm 0.03	6.66 \pm 0.03	142.57 \pm 0.04	65.44 \pm 0.04
	May	33.4 \pm 1.68	83.8 \pm 3.15	5.38 \pm 0.04	5.31 \pm 0.03	32.12 \pm 0.04	130.46 \pm 0.06	68.73 \pm 0.03
	June	32.1 \pm 1.70	87.9 \pm 2.08	24.02 \pm 0.03	22.55 \pm 0.07	38.83 \pm 0.03	178.45 \pm 0.07	72.43 \pm 0.04
Rainy	July	30.3 \pm 0.88	97.9 \pm 1.99	33.91 \pm 0.03	34.68 \pm 0.03	62.18 \pm 0.03	170.78 \pm 0.03	70.07 \pm 0.04
	August	28.7 \pm 1.16	89.9 \pm 2.01	37.73 \pm 0.04	36.81 \pm 0.03	68.68 \pm 0.03	179.35 \pm 0.07	73.77 \pm 0.04
	September	27.6 \pm 1.99	98.7 \pm 1.78	41.57 \pm 0.04	41.85 \pm 0.03	79.46 \pm 0.06	186.23 \pm 0.03	75.60 \pm 0.03
	October	26.9 \pm 1.31	92.7 \pm 1.93	35.81 \pm 0.04	35.12 \pm 0.06	65.55 \pm 0.07	188.20 \pm 0.07	77.91 \pm 0.04
Winter	November	23.7 \pm 0.09	85.7 \pm 0.89	12.05 \pm 0.01	12.92 \pm 0.03	29.37 \pm 0.04	204.07 \pm 0.04	82.84 \pm 0.03
	December	22.7 \pm 0.81	86.0 \pm 1.02	2.25 \pm 0.01	2.63 \pm 0.04	21.09 \pm 0.03	197.67 \pm 0.04	81.46 \pm 0.03
	January	21.8 \pm 1.01	97.8 \pm 0.95	1.24 \pm 0.04	1.05 \pm 0.04	11.74 \pm 0.04	195.46 \pm 0.03	78.38 \pm 0.04
	February	24.2 \pm 0.98	80.8 \pm 0.88	0.19 \pm 0.03	0.24 \pm 0.04	9.51 \pm 0.01	180.71 \pm 0.03	72.53 \pm 0.02

and Fisher's Z-transformation were performed to evaluate the statistical significance of the correlations (Snedecor & Cochran 1967).

Percent emergence and percent coupling were highest from July through October, when temperature ranged from 27–30°C and relative humidity from 90–98% (Table 1). Percent emergence and percent coupling peaked in September, when average temperature and relative humidity were near their highest, 27.6°C and 98.7%, respectively (Table 1). Percent emergence and percent hatching were lower from November through June (Table 1).

Probability values of the *t*-test demonstrate a statistically significant difference between percent male and female emergence, percent coupling, fecundity, and percent hatching between each season ($P < 0.01$). There is a positive correlation between the climatological factors (monthly temperature and relative humidity) and percent male and female emergence, percent coupling, fecundity, and percent hatching. However, *t*-tests and Fisher's Z-transformation indicated that the correlations are statistically not significant ($P = 0.01$).

The highest percent emergence and percent coupling, recorded in September, may be attributed to temperature (27.6°C) and relative humidity (98.7%), which apparently are optimal during this month and may possibly stimulate the reproductive physiology of the diapausing pupae. The lower percent emergence and percent coupling recorded during November through June might be the result of lower temperatures and lower relative humidity during winter, and higher temperatures and lower relative humidity during summer. The adverse climatological conditions during winter and autumn may cause *A. mylitta* to diapause, resulting in poor emergence and poor coupling during these respective months.

Rogers and West-brook (1985) reported that 10°C temperature caused delayed adult emergence in *Homoeosoma electellum* (Hulst) (Pyralidae) during different years of study. Similarly, Slosser et al. (1984) observed that cooler temperatures during spring resulted in delayed emergences of *Anthonomus grandis* Boheman (Coleoptera: Curculionidae). Jolly et al. (1974) reported that percent emergence and coupling of *A. mylitta* were reduced by low temperature (10°C) and low relative humidity (20%).

We suspect that percent emergence of *A. mylitta* was lower in summer during our experiment because of high temperature coupled with comparatively low relative humidity. This hypothesis corroborates studies by Therrien and McNeil (1985) who observed above normal pupal mortality in *Agromyza frontella* Rond (Diptera: Agromyzidae) under conditions of high temperature and low humidity. We currently are studying the effect of temperature and relative humidity on mortality of diapausing pupae of *A. mylitta*.

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A "HEATHII" ABERRANT OF *MITOURA GRYNEA SWEADNERI*
(LYCAENIDAE: THECLINAE)

Additional key words: Florida, phenotype.

Various types of wing pattern aberrations are known for the Theclinae, including a recurring phenotype with greatly exaggerated white maculation on the ventral wing surfaces. Fletcher (1903, 1904) misinterpreted such an aberrant female specimen of *Satyrium calanus falacer* (Godart) as a new species, describing it as *Thecla heathii*. Ironically, Fletcher soundly discounted the possibility that *T. heathii* represented an aberration of a known thecline, remarking "I can hardly think that it is a suffused albinic variety of any of them." Aberrant individuals of the Theclinae which possess exaggerated ventral white pattern elements are thus loosely termed "heathii" aberrations. A number of North American and European "heathii" phenotypes have been figured in the literature (e.g., Frohawk 1938, Muller 1976, Fisher 1976, Russwurm 1978, Baggett 1983, Ferris 1992). Fisher (1976) figured a "heathii" aberration of *Mitoura grynea castalis* (W. H. Edwards) from Texas. Ferris (1992) discussed and figured "heathii" aberrations of a related species of *Mitoura* (attributed to *barryi* Johnson). A "heathii" aberration of the Floridian subspecies *M. g. sweadneri* F. H. Chermock is herein reported for the first time.

On 23 September 1992, a male "heathii" phenotype of *M. g. sweadneri* (Figs. 1 & 2) was captured on the blossoms of *Bidens alba* (L.) DC (Asteraceae) at Yankeetown, Levy Co., Florida. The dorsal wing surfaces of the individual appear normal. In contrast, the ventral wing surfaces are extremely modified and asymmetrical. The postmedian bands of the forewings are reduced to several indistinct triangular subapical spots. The white postmedian bands of the hindwings are broken into rows of rounded spots in cells Cu_2 , Cu_1 and M_3 . These spots are surrounded by the remnants of the inner red bands. The red and white linear markings normally present in cells $2A$ are entirely lacking. Between veins M_3 and $SC+R_1$ the postmedian bands are enlarged and fused, becoming most pronounced in cells $SC+R_1$. The marginal white lines on the hindwings are expanded inwardly and transformed into rounded patches. In addition, the hindwings are disproportionately small in size. The ventral hindwing pattern of the aberrant *M. g. sweadneri* is similar in configuration to the "heathii" of *M. g. castalis* figured by Fisher (1976).

Fisher (1976) briefly speculated on the genetic and/or physical origin of the "heathii" aberration. Ferris (1992) suggested that this type of aberration may be the result of the expression of a homologous allele found in many theclines. Nijhout (1991) proposed that all the aberrations figured by Russwurm (1978), including two "heathii" phenotypes, are probably the result of temperature shock rather than recurring mutation. Environmental stress, such as temperature shock, has been shown to produce a variety of pattern aberrations (see Nijhout 1991). Additional research is required to more fully understand the cause of this intriguing abnormality.



FIGS. 1, 2. *Mitoura grynea sweadneri* (ventral). 1, male "heathii" aberration, Levy Co., Florida, 23 September 1992; 2, normal male, Hernando Co., Florida, 2 September 1989 (both leg. J. V. Calhoun).

The aberrant specimen of *M. g. sweadneri* is deposited in my personal collection in Dunedin, Florida.

I would like to thank two anonymous reviewers for helpful comments on the manuscript.

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TECHNICAL COMMENT

DANAUS CLEOPHILE (NYMPHALIDAE: DANAINAE) FROM JAMAICA

Regarding the record by Avinoff and Shoumatoff (1946) for *D. cleophile* from "Mt. Diablo," Vane-Wright, Ackery and Turner (1992) indicate that "the precise locality needs to be rediscovered." Their confusion understandably arose from the statement in the monumental work by Brown and Heineman (1972) that "it [*D. cleophile*] frequents the gulleys containing waterfalls . . . sailing down the slopes," giving my notes as its source. However, there was no such statement in my notes, nor have I seen any gulleys with waterfalls on Mt. Diablo, where apparently there are none. Our specimens were all taken (in 1940, not 1941) on a single, fairly level, approximately one-acre patch of open, tall grass, one or two miles north of Hollymount, along the east side of the road that rises to Hollymount. I understand from Turner, who knows the area well, that the lower part of that road now has been blocked and that a new road joins it somewhat lower than the point I have described, but that the habitat may be disturbed by felling of trees in connection with a bauxite project. It is noted that our capture of *D. cleophile* occurred some 50 years after the previous record by Godman and Salvin from "Moneague" (no reason to doubt that) and the description of its early stages (as interpreted by Brown and Heineman) in Clarendon by Pantón in 1893.

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BOOK REVIEWS

GUIA DE LAS MARIPOSAS DIURNAS DE GALICIA, by Eliseo Higinio Fernández Vidal. 1991. Excma. Diputación Provincial de A Coruña, Publicaciones. 291 pp., numerous color photographs and text figures. Hardcover, 24.5 × 29 cm, ISBN 84-86040-57-4. In Spanish. Available at a reduced price for lepidopterists from the author, Eliseo H. Fernández Vidal, Plaza de las Angustias, 4-2do; Ferrol 15403, La Coruña, Spain: \$20 U.S. plus postage (\$15 airmail; \$8 seamail).

Galicia is the region occupying the northwest corner of Spain and is wedged between Portugal to the south and the Bay of Biscay to the north, with the Atlantic Ocean to the west. It is one of the largest regions in the country, bigger than Belgium and Holland combined, and comprises four provinces: La Coruña, Lugo, Pontevedra, and Orense, of which only the latter does not border the sea. Culturally distinct from the rest of the country, Galicia lacks many of the familiar sights and sounds we Americans usually associate with Spain, such as bullfights and flamenco music and dancing. More or less isolated from the rest of the Iberian peninsula by mountain ranges on its southern and eastern borders, Galicia was never conquered by the Moors during the Middle Ages, and the region retains many ancient characteristics, including gallego—a language much older than the Castilian spoken elsewhere in Spain—as the predominant dialect. Today Galicia is dominated by cropland and managed woodlots, with only isolated patches of original forest scattered throughout its rolling hills. What remains of its original butterfly fauna had been little studied until the recent investigations of Eliseo Higinio Fernández Vidal.

Fernández Vidal is a native of Galicia, born in Ferrol, La Coruña, in 1944. Eleven years of service in the Merchant Marine brought him the opportunity to collect and observe butterflies in many places throughout the world, especially West Africa and South America. As a result, roughly one-third of his personal collection of nearly 14,000 specimens is tropical. But in 1974, Fernández Vidal decided to turn his attention to the butterflies of his native land, and he embarked on a detailed study of “la fauna gallega de mariposas.” Convinced of the importance of careful field work, Fernández Vidal has devoted considerable time to exploring Galicia first hand, observing, photographing, and collecting its butterflies. The knowledge gained from these endeavors is being used to prepare a definitive two-volume work on the biology, ecology, and distribution of the butterflies of Galicia. The book reviewed here is a synopsis of this larger, as yet unpublished, effort and is designed as an easy-to-use guide for beginning lepidopterists and naturalists. As such, it succeeds admirably.

The book has two main sections and four appendices. The introductory first section (Las Mariposas) summarizes basic information about butterflies: classification and nomenclature, life cycle, adult morphology (including markings, scales, colors, and sexual dimorphism), bionomics (phenology, habitats, diapause), special habits (cannibalism, myrmecophily, gregariousness, pest status, etc.), geographical distribution, and conservation and protection of endangered species. Most of these topics are illustrated by well-executed line drawings.

The second and largest section (Claves y Fichas Especificas) provides dichotomous keys to families and genera, followed by detailed species accounts. The lack of keys to species is not really a drawback, especially for the Papilionidae, which has only one gallegan species for each of the four genera represented, so that generic keys serve as specific keys. For other groups, the generic keys are supplemented by clear drawings of important features to help separate easily confused species (e.g., differences in male tibial spurs and wing maculations between *Plebejus argus* and *P. idas*). At the end of each family section is a collection of photographs of live butterflies and caterpillars. These vary widely in quality from excellent (a few) to poor (many), the latter usually blurry from poor focusing, shallow depth of field, or subject movement. Use of an electronic flash would have improved clarity and sharpness tremendously. Photographs of pinned specimens of all species in the family, grouped and mounted over beige graph paper at much less than life size, complete each color section. These are uniformly of better clarity than the photographs taken in the field. The species accounts include entries for the following

categories: morphological description, habitat, foodplant, distribution, and subspecies. No common names are given, for the simple but surprising reason that no popular common names for butterflies have evolved in Galicia!

The four appendices provide a hint of the kind of useful data and detailed analysis to be presented in the forthcoming two-volume work. Appendix I discusses the origin, establishment, and composition of the butterfly fauna of Galicia in terms of geographic realms, fossil history, and Miocene and Pliocene refugia and dispersal routes. It concludes with a table that lists for each gallegan species Fernández Vidal's assessment of its geographical origin, geological time of establishment, and the probable route of passage by which it entered the region.

Appendix II is a checklist of butterflies of Galicia and their occurrence in the four provinces. There are 155 species recorded from the region, distributed among the provinces as follows: Lugo (146 species), Orense (133), Pontevedra (94), and (ironically) in Fernández Vidal's home province of La Coruña (92).

In Appendix III is given the date of the discovery of each of the species in the region, listing them chronologically in order of the published documentation of their occurrence in Galicia, from 1866 through 1991. Of the 155 species, Fernández Vidal himself has documented 40 between 1977 and 1991, including 18 reported for the first time in this book. In addition, Fernández Vidal has named thirteen new subspecies and forms from Galicia during this time period.

The final Appendix (IV) is a bibliography of the butterflies of Galicia, which contains only 31 entries. Significantly, fully half of the cited publications (15) are authored by Fernández Vidal, underscoring his important contribution to the better understanding of the butterflies of this little-known region of Spain.

The book is sturdily bound and attractively designed. There is an index to species, but not one to subjects—a major drawback. Although the photographs are not first-rate, the line drawings are excellent. Much of the information presented here is new and, especially in the appendices, of great interest. Of course, those unable to read Spanish will find much of this interesting information inaccessible. Although this book is an excellent introduction to the butterflies of Galicia, I look forward to the appearance of the more detailed two-volume publication with its greatly expanded coverage of the topics that are treated briefly, but tantalizingly, in the appendices of the present work.

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THE OWLET MOTHS OF OHIO—ORDER LEPIDOPTERA, FAMILY NOCTUIDAE, by Roy W. Rings, Eric H. Metzler, Fred J. Arnold, and David H. Harris. 1992. Bulletin of the Ohio Biological Survey (new series) Vol. 9, no. 2. vi + 223 pp., 8 color & 8 B/W plates. Softcover, 21.5 × 28 cm, ISBN 0-86726-110-8. \$20 (+ \$3 p & h). (Order from Ohio Biological Survey, 1315 Kinnear Road, Columbus, Ohio 43212-1192; Ohio residents add 5.75% tax.)

The appearance of this book in 1992—along with *The Butterflies and Skippers of Ohio* by D. Iftner, J. Shuey, and J. Calhoun—marks the first substantial fruits of what is probably the most well-organized state faunistic survey of Lepidoptera ever undertaken in the Americas. The book is an annotated checklist for 708 species of Noctuidae, but it is also much more.

Introductory sections include an abstract, acknowledgments, lists of figures and plates, and an Introduction giving historical perspective. Sections follow that are useful to users, from beginner to professional: Nomenclature and Systematics, Collection and Preservation of Specimens (accompanied by Ohio map of counties), Identification of Owllet Moths

(emphasis on wing and genitalic features), and Developmental Biology of Owlet Moths (an overview of noctuid life histories). A short essay on Conservation of Owlet Moths follows, indicating threats to populations by habitat loss, pesticides, and human exploitation. A tone of responsible stewardship of moth populations is projected, with an appeal to collectors to inspect netted specimens before killing only those wanted, to release gravid females, and to collect selectively at lights. Gardening practices to foster Lepidoptera breeding are recommended. Land management practices by state government parks and wildlife agencies to protect Lepidoptera are acknowledged and recommended (specific recommendations appear in the Descriptions of Special Habitats section later in the book).

Next comes a systematic checklist of the species, arranged according to the R. Hodges et al. (1983) *Check List of Lepidoptera of America North of Mexico*, but with modifications reflecting changes and additions since that work was published. Then the meat of the book: species treatments, with Hodges and McDunnough checklist numbers, scientific names (no English names), author name and date of publication, references to books illustrating the moths (and corrections of names used in them when needed), Status (rare, common, etc.), History (dates of earliest and latest records), and Host (food-plant references and new host records, if known). A Remarks entry with useful identification notes or nomenclatural annotations is added for less than half of the species treated. A miniature Ohio map with dots for county records accompanies each species entry. In the right margin are two bars (one for northern and the other for southern counties), each divided into squares for months of the year. These are variously shaded to represent number of capture records, ranging from white for no records, and increasingly darker for 1–3 records and 3–10 records, to black for more than 10 records. There are usually 5–7 species treatments per page.

Next comes a section entitled "Owlet moths that qualify for special attention in Ohio." It lists one species (*Catocala pretiosa*) as Extirpated, 13 as Endangered, 5 as Threatened, 13 as rating Special Concern, 40 under Status Unknown, and 44 as species of Special Interest. Those already officially listed as Endangered by the Ohio Department of Natural Resources, Division of Wildlife, are indicated with an asterisk. Explanations of each category are explained. Following this listing is a description of eight habitats that contain significant numbers of species deserving concern, and why each is at risk. Recommendations for improved management of these preserves are given.

Short sections follow listing migrant species, a list of species expected but not yet recorded (hypothetical checklist), and list of species excluded from the list (with reasons in seven categories for exclusion). An alphabetical list of host plants is given next, with noctuid species listed that reportedly feed on them. A glossary, a list of regional lepidopterists' societies, Ohio county abbreviations, literature cited, bibliography of "useful publications in the study of Noctuidae," a checklist to Hodges et al. (1983) *Check List* numbers (moths listed alphabetically), and general index round out the text.

There are 16 plates, the first 8 of which are black and white photos of eggs (I–III) and larvae (IV–VIII). The rest are composite color plates of owlet moths specially selected as not illustrated previously in color, or shown next to closely similar species for better comparison (criteria for selection listed on page 6).

Besides being a thorough and carefully prepared annotated checklist for Ohio Noctuidae, this book is loaded with biological and taxonomic information. It brings up to date the nomenclatural changes since publication of the Hodges et al. *Check List* of 1983 (notably R. Poole's 1989 *Lepidopterorum Catalogus*, New Series, covering worldwide Noctuidae) and lists other recent literature pertinent to Ohio Noctuidae. It functions as a manual for tougher species, with identification aids in the text and sharp life-size color photos of moths such as *Zanclognatha* and *Renia* species that are troublesome to identify. The sections dealing with species and habitats of concern are unique, wedding interests of the lepidopterist to those of the people and institutions concerned with natural resources management and protection. The sheer numbers of records—garnered through visits to museums and extensive collecting by members of the Ohio Lepidopterists and other collaborations—make coverage of range, flight periods, and status more authoritative than in any previous state faunal list of moths.

I highly recommend this book to anyone interested in eastern North American moths

and as a model faunistic study for emulation in any geographic area. Companion works on other moth families are planned, and when completed will provide coverage of Lepidoptera unexcelled by that of any other American faunistic study.

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47(3), 1993, 253-254

BIOLOGIA Y MORFOLOGIA DE LAS ORUGAS. LEPIDOPTERA. VOL. 9. NYMPHALIDAE—SATYRIDAE—LYCAENIDAE—ZYGAENIDAE, by Carlos Gomez de Aizpurua. 1991. Boletín de Sanidad vegetal. Fuera de Serie No. 21. Ministerio de Agricultura, Pesca y Alimentación, Centro de Publicaciones, 1 Paseo de la Infanta Isabel, 28014 Madrid, Spain. Softcover, 18.5 × 25 cm, 226 pp., text in Spanish. 3000 pesetas (about \$30.00 U.S.).

This book is one of a series of volumes on the immatures of Spanish Lepidoptera. It includes a map for each species; a chart of the months of presence for eggs, larvae, pupae, and adults; a little about the habits of adults and immatures; and a brief mention of hostplants. But most of the text consists of lengthy descriptions of the colors of older larvae, pupae, and adults, with each stage illustrated by photographs. Unfortunately, descriptions and photographs of eggs and young larvae are not included and the book lacks such rigorous systematic niceties as morphological descriptions and setal patterns of larvae and pupae. Not all Spanish butterflies are included, and some groups are poorly represented (only one species of Melitaeini, for instance). Zygaenidae are included (Europeans treat burnet moths like butterflies because of their abundance and colorful appearance).

The book's best feature is its nice photos of older larvae and pupae. The photos are high quality, with most of each animal in sharp focus, permitting valuable comparisons with larvae and pupae of other species in other localities. In leafing through the photos, I was amazed to note that the larva of *Hipparchia statilinus* appeared identical to the larva of "*Neominois*" *ridingsii* I was rearing from Colorado, complete with the same head and body pattern and the same dark subdorsal mid-body stripe above a pink stripe. Comparison of *ridingsii* under the microscope with the photos did reveal some difference (the pink stripe of *ridingsii* is actually one stripe position lower than the pink stripe of *statilinus* and corresponds to the white spiracular stripe of *statilinus*). But surely the amazing larval resemblance must be due to phylogenetic relationship rather than to coincidence, and indeed Lee Miller (1968, Mem. Amer. Ent. Soc. 24, p. 119) placed both genera next to each other within tribe Satyrini of his family Satyridae, based on adult traits. I will be bold here, and declare that *ridingsii* is really *Hipparchia* (*Neominois*) *ridingsii*. (Furthermore, the Himalayan *Karanasa* is very close to *Neominois* according to Miller and others, so it should be demoted to a subgenus of *Hipparchia* as well.) Because generic limits are arbitrary, surely the color patterns of larvae and pupae can help harmonize the differing generic concepts in America and Europe.

The larva of *Erebia meolans* is similar to American *E. epipsodea*. The pupa and adults of Spanish *Celastrina argiolus* resemble Colorado C. "*neglecta*" more than Colorado C. "*lucia*-type," which could help in determining whether any American form deserves the name *argiolus*. The theory that American *Lycaena phlaeas americana* came from Europe by ship suffers a setback because photographs of the Spanish adults (and English and other European adults I have seen) show the tails too long and the underside too brown to match American *americanus*; only ssp. *polaris* from Lapland has the underside gray enough and the tails short enough to match *americana*, but it has a brassy upperside. For this theory to hold water, a European population will have to be found that matches *americana*. A further setback for the theory: proponents of ship transport cite *americana*'s use of introduced European *Rumex acetosella* in America and Europe as proof, but

Colorado *Lycaena xanthoides editha* prefer it to native hosts also, evidently because of its larger leaves.

These are just a few of the interesting speculations to be made and conclusions to be drawn from comparing early life stages of different taxa across localities—a task made easier by the publication of collections of high quality color photographs such as this one.

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OBITUARY

THOMAS WILLIAM DAVIES (1915-1990)

Thomas William Davies, a Charter Member of the Lepidopterists' Society, died on 19 August 1990, of lung cancer, at his home in San Leandro, California. Through self-education Tom developed an extensive knowledge of the world Lepidoptera, and he assembled a very large private Lepidoptera collection. Employed by the California Academy of Sciences between 1966 and 1990, Tom was the Academy's authority on Lepidoptera. It was Tom's wish that his collection become a part of the Academy's collection and in May 1988 it was transferred from his home to the Department of Entomology.

Tom was born in Stockton, California, on 29 April 1915, the eldest of three sons of William Thomas Davies, a native Californian from Stockton, and Catherine "Kitty" Blanche Davies, who was of Scottish ancestry but born in England.

Tom attended public schools in Oakland and graduated from Roosevelt High School in 1933. Tom's brother Stanley recalls that Tom was actively "collecting butterflies and all sorts of other things" when he was 12 or 13 years old. Stanley, who was three years younger than Tom became skilled in collecting butterflies for his older brother and later made some significant collections for Tom. William "Bill" A. Hammer, Tom's lifetime friend and lepidopterist colleague for over 55 years, a retired engraver, also of San Leandro, California, recalls that they first met through a mutual friend, Verner Carlson, when they were seniors in high school. Tom and Bill were interested in collecting butterflies and the eggs of wild birds. At that time one could easily go into the Oakland Hills to shoot squirrel and cottontails with BB guns and .22 rifles, which they did. When birds were shot, Bill, who was interested in taxidermy, would mount them in a professional manner. Later they turned their interest more to the collection of Lepidoptera. Their first collections were made in the Oakland Hills near their homes, and then in the Santa Cruz Mountains, using Bill's Stutz touring car for transportation.

Following graduation from high school Tom's first job during the depression years was with a bakery in Oakland. He lost it for having given some day-old bread to a disadvantaged person—the company did not want to attract poor people to their premises. Then followed various employment, including carpenter and welder. In 1940 he started employment with the Southern Pacific Railroad Company in Oakland, working in the switching yard, where he became a foreman. During the Second World War Tom was not drafted into the military because railroads were considered essential industry and vital to the war effort.

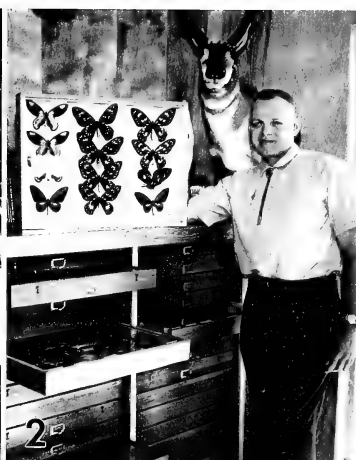
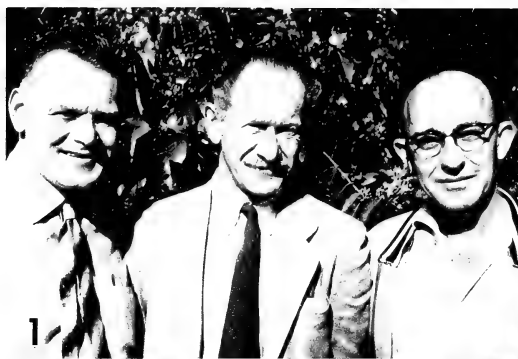
Tom married Mary Alice Little on 20 September 1938. Mary Davies has commented that she was unaware that Tom collected butterflies until after they were married.

In 1955, a tragic accident in a railroad yard nearly ended Tom's life, and yet the loss of both legs below the knees did not deter him from living a very full and active life thereafter.

Following his recovery, persons who met Tom were unaware of his use of prosthesis, and it certainly did not deter him from the extensive field work that he undertook both in this country and abroad, including Australia, Malaysia, Papua New Guinea, and other parts of the tropical world.

In order to acquire Lepidoptera Tom's early correspondents included Robert G. Wind, of Berkeley, California; Pedro Paprzycki of Satipo, Peru; M. Spelman, of the Nature Room Supply House; and W. F. H. Rosenberg, of Edgware, England. Later it included Rodrigo Rodrigues, of Palawan, Philippines, and many others, who might supply butterflies, especially world Papilionidae, including the birdwings, and the *Delias* in the Pieridae. Tom also exchanged extensively and sold duplicates from his collection. In addition he acquired many of the basic books and papers to identify butterflies and moths, including the Seitz series.

Tom was 24 years old when he first visited the Entomology Department at the California Academy of Sciences in 1939. On 9 August he had written to the Department of Entomology, and received a response from the curator, Edward Payson Van Duzee, that he would be welcomed to visit the department. It was some 25 years later, in the mid-1960's,



that Tom, on the suggestion of Lloyd L. Martin of the Los Angeles County Museum of Natural History, began volunteering in the Academy's Department of Entomology. After a year or two, funds became available for his employment as a result of a U.S. Department of Agriculture grant that I had received. Fortunately, after these funds expired, the Academy, which urgently needed Tom's talents in Lepidoptera, funded his employment on a part-time basis to curate its Lepidoptera collection.

Tom's early collecting colleagues in the Bay Area were William A. Hammer, Robert and Clo Wind, Rodney Davis, and his brother Stanley Davies. His later Bay Area Lepidoptera associates included Richard M. Brown, Robert L. Langston, C. Don MacNeill, Jerry A. Powell, Herman G. Real, Harriet V. Reinhard, Jon H. Shepard, Jeffrey A. Smith, James W. Tilden, Keith Van Wolfe, Tom's son William T. Davies and myself. Tom's notebook indicates that he visited the elderly lepidopterist and retired police officer, Mr. James Edward Cottle (1861–1953) of Hayward, on 30 April 1946. Tom was later to receive through his friend Bill Hammer a fine series of the extinct Xerces Blue and other butterflies from the Cottle collection that Bill in turn received from Kenneth Rand. Other collecting colleagues and guests to Tom's home included Dr. Jean Marie Cadieu, J. Donald Eff, Isao Hashimoto, Lloyd M. Martin, Dr. Charles L. Remington, P. Sheldon Remington, Dr. Laurent Schwartz, Raymond Straatman, Dr. Norman B. Tindale, and Colin W. Wyatt.

With the advent of the Second World War, Tom's brother Stanley was inducted into military service and in 1943 was stationed with the 9th Station Hospital on Guadalcanal Island in the Solomon Islands. Stanley had earlier collected for Tom, including the Acapulco area of Mexico in 1939. With his earlier training in collecting Lepidoptera, Stanley decided to make a collection of the butterflies of his area of Guadalcanal for Tom. Even though there was a tight censorship and the use of APO numbers at the time, with the shipments of butterflies received from Stanley, Tom knew by the taxa received where his brother was stationed in the Pacific. Stanley later in 1943 collected also in Okinawa.

Tom's first field notes recorded a trip to collect butterflies on 8 July 1933 to Highland Creek, Sand Flats, 6500 feet, above Dorrington, in California's Sierra Nevada. Tom was to make hundreds of collecting trips in the following 55 years, in California, Arizona, Nevada, Colorado, New Mexico, Montana, Wyoming, Alberta, and overseas, including the Fiji Islands, New Caledonia, Malaysia, Papua New Guinea, Australia, and New Zealand. Some of Tom's favorite collecting areas in the Bay Area included Mitchell Canyon, on Mount Diablo in Contra Costa County, and Frank Raines Park area in Del Puerto Canyon, east of Mount Hamilton in Stanislaus County.

In the early 1950's Tom and his friend Bill Hammer joined Lloyd Martin and Dr. W. P. Comstock, in summer field work in Madera Canyon and other areas in Arizona.

As a result of Tom's and Mary Kay's (his daughter) visit to the Bishop Museum's Wau Ecology Institute, on the island of New Guinea, in 1970, Mary Kay met and subsequently married Peter Shanahan, an entomologist/naturalist and neighboring coffee planter to the Wau Ecology Institute. Since Tom could not be present at the wedding, Dr. J. Linsley Gressitt gave the bride away in a garden wedding ceremony in 1971. Tom was to make

←

FIGS. 1–7. 1, Left to right, Thomas W. Davies, Colin W. Wyatt, and William A. Hammer, San Leandro, California, 10 January 1959; 2, Thomas W. Davies with drawer of birdwing butterflies at his home in San Leandro, California, March, 1962 (Morning News photo); 3, Charles L. Remington (left) and Thomas W. Davies examining specimen of Nymphalidae at Tom's home in San Leandro, 1968 (photo by Paul H. Arnaud Jr.); 4, Isao Hashimoto (right) and Thomas W. Davies at Nami Creek, Mount Kaindi, Morobe District, Papua New Guinea, 2 April 1973 (photo by Peter Shanahan); 5, Thomas W. Davies and grandson Thomas W. Davies at light table at home, San Leandro, 1983 (photo by William T. Davies); 6, Thomas W. Davies photographing paper wasp nest, Butterfly Lane, Kuranda, Queensland, Australia, 5 July 1984 (photo by Mary Kay Shanahan); 7, Photography session, Southwestern Research Station, Portal, Arizona, August, 1985, left to right, Thomas W. Davies, Robert W. Mitchell, Edward S. Ross, and Paul H. Arnaud Jr. (photo by Paul-Henri F. Arnaud).

two subsequent visits to Wau in the 1970's prior to the Shanahan's move to Australia in 1975. These visits which totaled over six months, permitted Tom to collect extensively in the region of Wau/Bulolo. Tom's collection which included over 26,204 (7486 spread, 18,718 papered) Papua New Guinea Lepidoptera, mostly butterflies and skippers, as well as the specimens collected by Peter and Mary Kay Shanahan, are acknowledged by Michael Parsons (1991) in his recent book, *Butterflies of the Bulolo-Wau Valley*. Some of Tom's favorite groups in Papua New Guinea, in addition to the Birdwings and other Papilionidae, were the *Delias* of the Pieridae and the Jewel Moths of the genus *Milionia* of the Geometridae. Fine series of these become a part of his collection both from his own and the Shanahan's collecting.

Between 19 March 1965 and 1990 the California Academy of Sciences received from Tom 153,628 insect and other arthropod specimens in 607 dated transactions. Of these specimens at least 91,026 were Lepidoptera (43,544 spread and 47,482 papered).

In addition to specimens deposited in the California Academy of Sciences there are many Davies' specimens deposited in other institutions, as the Los Angeles County Museum of Natural History and Yale University, and private collections.

Tom prepared the specimens for the impressive display of "Rainbow of Butterflies" that first greets the eyes of visitors to the Academy's Kathryn Clarke Kendrick Insect Room Exhibit, which was dedicated on 13 February 1981. These were prepared so as to avoid the presence of pin marks that can result from the spreading of specimens. In February, 1986, Tom designed and prepared over 250 specimens used in the decoration of permanent displays of butterflies in the Majestic Hotel, at 1500 Sutter Street, in San Francisco. He also prepared entomological material that was displayed by the Academy at the United Airlines Terminal of the San Francisco International Airport.

Tom's first quality camera was a German-made EXA that he acquired in July 1954, but he did not undertake serious biological photography until the later 1960's. With advice from the Academy's nature photographer, Dr. Edward S. Ross, Tom expanded his interest in insect and nature photography. He built a large file of 35 mm colored slides, including many lepidopterous life histories, as well as slides of natural history subjects from both western North America and his foreign travels.

Tom's photographs have appeared in books published by Audubon, Chanticleer Press, Inc., GEO, Grolier, Inc., National Geographic, Pacific Discovery, Silver, Burdett, & Ginn, Inc., Stokes Publishing Company, and Time-Life. He donated some colored slides to the Academy's Department of Entomology for its use, but the greater part of his photographic collection is with his son, William T. Davies.

Tom's publications covered the oviposition of *Archilestes californica* MacLachlan (Davies 1972); the treatment of the genus *Polygonia* (Davies 1975) in Howe's *The Butterflies of North America*; a list of the butterflies of Mt. Kaindi, New Guinea (Davies 1978); on a remarkable aberrant female of *Speyeria nokomis nokomis* (Edwards) (Davies & Arnaud 1967) with a colored plate; obituaries on Robert Grant Wind (Arnaud & Davies 1976) and Hardin Blair Jones (Arnaud & Davies 1981); and on *Entomobrya kanaba* (Wray) as an indoor house pest in central California (Arnaud & Davies 1980).

Several insects were named in Tom's honor, including *Melitaea leaneri daviesi* Wind, 1947 (Lepidoptera: Nymphalidae, from Strawberry Lake, Tuolumne County, California); and *Pararhodia daviesorum* Lemaire, 1979 (Lepidoptera: Attacidae; from summit of Mount Kaindi, 13 miles S of Wau, Morobe District, Papua New Guinea; named after Tom and his daughter Mary Kay).

Tom is survived by his wife Mary Alice Davies to whom he was married for nearly fifty-two years; a son William Thomas Davies of Norden, California; two daughters, Mary Kay Grosvald of Tulsa, Oklahoma, and Nancy Susan Davies of Bell Canyon, California; his brother Stanley G. Davies of Burson, California; and three grandchildren, Erin M. Chavez of Bell Canyon, and Thomas William Davies and Cathryn Alyssa Ardith Davies of Norden.

ACKNOWLEDGMENTS

Thanks are extended to Mrs. Mary Alice Davies and Mr. William A. Hammer, of San Leandro, California; Ms. Nancy S. Davies, of Bell Canyon, California; Mr. Stanley G.

Davies, of Burson, California; Mr. William T. Davies, of Norden, California; Mrs. Mary Kay Grosvald, of Tulsa, Oklahoma; Mrs. Madeline M. Arnaud, Mrs. Helen K. Court, Dr. David H. Kavanaugh, Mr. Vincent F. Lee, Dr. C. Don MacNeill, Ms. Julieta F. Parinas, Dr. Edward S. Ross, and Mrs. Stella E. Tatro, of the Department of Entomology, California Academy of Sciences, for information, editorial assistance, review of the manuscript, and other help in the preparation of this article. I would also like to thank Ms. Caroline Kopp and Ms. Charlotte Fiorito of the Photography Department, California Academy of Sciences, for their photographic assistance with the illustrations.

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ADDENDUM ET CORRIGENDUM TO VOLUME 46

ADDENDUM TO MACNEILL (1992)

In his recent obituary of Pepe Herrera, MacNeill (1992, *J. Lepid. Soc.* 46:248–254) inadvertently omitted Herrera's last publication. It should be cited as follows:

JOHNSON, K., L. D. MILLER & JOSÉ HERRERA G. 1992. *Eiseliana* and *Heoda*, high Andean and austral genera of the Neotropical Eumaeini (Lepidoptera: Lycaenidae). *Atca Entomol. Chileana* 17:107–146.

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CORRECTION TO MATHER & MUNROE (1992)

In Mather and Munroe (1992, *J. Lepid. Soc.* 46:159–160), the generic name *Hileithia* (Pyralidae) was misspelled twice in the text as "*Hiliethia*." The editor apologizes for this mistake.

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Contributions to the *Journal* may deal with any aspect of Lepidoptera study. Categories are Articles, Profiles, General Notes, Technical Comments, Book Reviews, Obituaries, Feature Photographs, and Cover Illustrations. Reviews should treat books published within the past two years. Obituaries must be authorized by the President of the Society. Requirements for Feature Photographs and Cover Illustrations are stated on page 111 in Volume 44(2). *Journal* submissions should be sent to the editor at the above address. Short manuscripts concerning new state records, current events, and notices should be sent to the *News*, Stephanie McKown, Editor, 650 Cotterell Drive, Boise, Idaho 83709 U.S.A. For information regarding book reviews, contact Boyce A. Drummond, Natural Perspectives, P.O. Box 9061, Woodland Park, CO 80866. *Journal* contributors should submit manuscripts in *triplicate*, typewritten, *entirely double-spaced*, with wide margins, on one side only of white, letter-sized paper. Prepare manuscripts according to the following instructions, and submit them flat, not folded.

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SHEPPARD, P. M. 1959. Natural selection and heredity. 2nd ed. Hutchinson, London. 209 pp.

— 1961a. Some contributions to population genetics resulting from the study of the Lepidoptera. *Adv. Genet.* 10:165–216.

Illustrations: Only half of symmetrical objects such as adults with wings spread should be illustrated, unless whole illustration is crucial. Photographs and drawings should be mounted on stiff, *white* backing, arranged in the desired format, allowing (with particular regard to lettering) for reduction to fit a *Journal* page. Illustrations larger than letter-size are not acceptable and should be reduced photographically to that size or smaller. The author's name and figure numbers as cited in the text should be printed *on the back* of each illustration. Figures, both line drawings and photographs, should be numbered consecutively in Arabic numerals; "plate" should not be employed. Figure legends must be typewritten, double-spaced, *on a separate sheet* (not attached to illustrations), headed EXPLANATION OF FIGURES, with a separate paragraph devoted to each page of illustrations. Color illustrations are encouraged; contact editor for submission requirements and cost.

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Cover illustration: The eastern tiger swallowtail (*Papilio glaucus* L.) is one of the largest North American butterflies. It is a widespread species of the eastern United States. Original drawing by Ron Klingner, 3814 Paul Mill Road, Ellicott City, Maryland 21042.

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PHYLOGENY AND BIOGEOGRAPHY OF *EUPHYES* SCUDDER (HESPERIIDAE)

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ABSTRACT. The 20 species of *Euphyes* were analyzed phylogenetically and were found to fall into four monophyletic species groups, each of which is defined by one or more apomorphic characters. The *peneia* group contains *Euphyes peneia* (Godman), *E. eberti* Mielke, *E. leptosema* (Mabille), *E. fumata* Mielke, *E. singularis* (Herrich-Schäffer), and *E. cornelius* (Latreille). The *subferruginea* group contains *E. subferruginea* Mielke, *E. antra* Evans, and *E. cherra* Evans. The *dion* group contains *E. dion* (Edwards), *E. dukesi* (Lindsey), *E. bayensis* Shuey, *E. pilatka* (Edwards), *E. berryi* (Bell), and *E. conspiciua* (Edwards). The *vestris* group contains *E. vestris* (Boisduval), *E. chamuli* Freeman, *E. bimacula* (Grote and Robinson), and *E. arpa* (Boisduval and Leconte). *Euphyes ampa* Evans could not be placed confidently within this framework.

Geographic distribution of each species group suggests that exchange between South America and North America took place at least twice. The two Caribbean Basin species (*E. singularis*, *E. cornelius*) share a common ancestor with *E. peneia*, a species found in Central and South America. This suggests a vicariant event involving Central America and the Greater Antilles. The *dion* and *vestris* groups show strong patterns of allopatric differentiation, suggesting that the isolation and subsequent differentiation of peripheral populations has played an important role in the development of the extant species.

Additional key words: evolution, cladistics, wetlands, vicariance biogeography, population differentiation.

The genus *Euphyes* Scudder as previously defined included a heterogeneous assemblage of skippers distributed throughout the New World (Evans 1955, Mielke 1972). I recently demonstrated that *Euphyes* was paraphyletic with respect to *Problema* Skinner and Williams and I redefined the two genera monophyletically, resurrecting the genus *Arotis* Mabille in the process (Shuey 1987). *Arotis* and *Problema* appear to represent sister genera defined by the unique shape of the female eighth abdominal tergite and the heavy armature of the aedeagus. The resurrection of *Arotis* removed seven species from *Euphyes* [*Arotis sirene* Mabille, *A. derasa* (Herrich-Schäffer), *A. kayei* (Bell), *A. mapirica* (Bell), *A. pandora* (Lindsey), *A. bryna* (Evans), and *A. evansi* (Mielke)].

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Arotis and *Problema* together form the probable sister group of *Euphyes*.

As redefined, *Euphyes* consists of 20 species with 3 centers of endemism: central South America, the northern Antilles, and eastern North America. In this paper I construct a detailed phylogenetic hypothesis for *Euphyes* and relate species distributions to it.

MATERIALS AND METHODS

I examined material of all available species. Because some of the South American species are rare, several species were not available in North American museums for examination. However, Mielke (1972, 1973) figures these species allowing me to tentatively assign some character states without examining specimens. Unless otherwise indicated, I critically examined 20 or more specimens of each sex, chosen to encompass most of the range of each species. Material which was less critically examined generally exceeded 100 specimens or more per species. Species examined include: *E. arpa* (Boisduval and Leconte), *E. pilatka* (Edwards), *E. dion* (Edwards), *E. dukesi* (Lindsey), *E. conspicua* (Edwards), *E. berryi* (Bell), *E. bayensis* Shuey, *E. bimacula* (Grote and Robinson), *E. singularis* (Herrich-Schäffer), *E. vestris* (Boisduval), *E. cornelius* (Latreille), *E. peneia* (Godman), *E. chamuli* Freeman, and *E. subferruginea* Mielke.

I identified 29 morphological characters, including structures of the female and male genitalia, male stigma, and wing pattern. Characters were polarized using the genera *Problema* and *Arotis* as out-groups. This choice was based on a prior analysis which indicated that these two genera together comprised the sister group to *Euphyes*. The data set of 29 characters and 18 operational taxonomic units (OTUs) was analyzed using the "Penny" program from the PHYLIP 2.7 Metro package (Felsenstein 1984), which uses Wagner parsimony. The data set was analyzed five times using different random seed numbers as recommended by Felsenstein.

CHARACTER ANALYSIS

The morphological characters employed in the analysis include 9 characters of the female genitalia, 14 male secondary sexual characters, and 6 characters of the wings. Table 1 summarizes the character state distributions for each species. The figures emphasize North American, Caribbean, and common South American species. Comparative figures of South American species can be found in Mielke (1972, 1973).

Female Genitalia Characters

In the underived condition the ductus bursae is a completely sclerotized, short, straight tube and the corpus bursae is a short, blunt sac.

TABLE 1. Character matrix for *Euphyes* species. Character numbers refer to character numbers in text. 0 = plesiomorphic character state. 1 = derived character state. ? = unknown character states.

OTU's	CHARACTER NUMBERS																												
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29
out-group	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>bayensis</i>	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0
<i>dion</i>	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0
<i>dukesi</i>	0	1	1	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1
<i>berryi</i>	0	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0
<i>pilatka</i>	0	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	1	0	1	1	0	0	0	1	0	1	1	0
<i>conspicua</i>	0	1	1	0	0	0	0	1	1	0	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0
<i>vestris</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0
<i>chamuli</i>	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0
<i>arpa</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	1	0	1	0	0
<i>bimacula</i>	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	1	0	0
<i>peneia</i>	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
<i>singularis</i>	0	1	1	0	1	1	0	0	1	1	0	1	0	0	0	0	0	1	1	1	0	1	1	1	0	0	0	0	0
<i>comelius</i>	0	1	1	0	1	0	1	0	0	1	0	1	1	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0
<i>fumata</i>	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
<i>eberti</i>	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
<i>leptosema</i>	0	1	1	0	1	0	0	0	1	0	0	1	0	0	0	0	0	0	0	?	0	0	0	0	0	0	0	0	0
<i>subferruginea</i>	0	1	?	0	?	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0

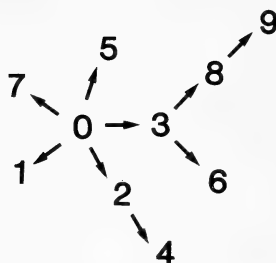


FIG. 1. Hypothesized transformation of female genitalic characters. 0 is plesiomorphic condition. All other numbers are derived and refer to character numbers in text.

The hypothetical derivations of the following apomorphies are shown in Fig. 1.

1. Ductus bursae unsclerotized dorsally (Figs. 2–5). This condition is found in *E. vestris* and *E. chamuli*.

2. Corpus bursae elongate (Figs. 4–25). This character is found in all *Euphyes* except *E. vestris*.

3. Ductus bursae elongate (Figs. 6–21). This character is found in the *dion* and *peneia* groups. Based on Mielke's (1972) figures, this character state may be present in the *subferruginea* group.

4. Corpus bursae very elongate (Figs. 22–25). This condition is found in *E. arpa* and *E. bimacula*.

5. Ductus bursae with lateral projections (Figs. 16–21). This condition characterizes the *peneia* group. Based upon Mielke's (1972) figures, this character state may be present in the *subferruginea* group, but has been coded as "?" for this group in the data set.

6. Ductus bursae with a slight bend posteriorly (Figs. 18 & 19). This condition is an autapomorphy for *E. singularis*.

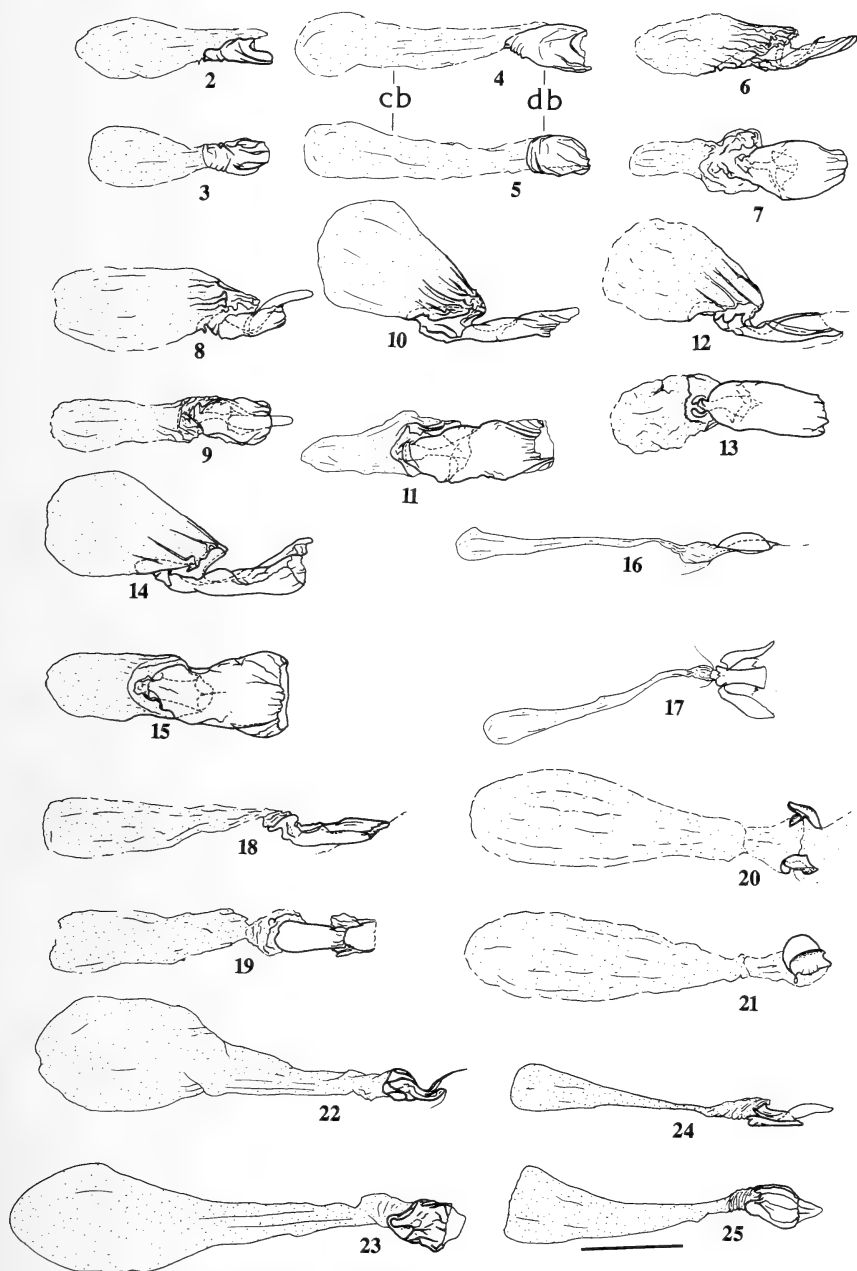
7. Ductus bursae unsclerotized (Figs. 20 & 21). This character is interpreted as a autapomorphy for *E. cornelius* where the only sclerotized regions of female genitalia are lateral extensions of the ductus bursae (character 5).

8. Ductus bursae doubled back upon itself (Figs. 6–15). This condition characterizes the *dion* group.

9. Corpus bursae erect (Figs. 10–15). This character state defines a clade within *dion* group composed of *E. conspicua*, *E. pilatka*, and *E. berryi*. Because neither this character state nor the alternative character state (corpus bursae not erect) occur in the out-group, the polarization of this and the alternate state (Figs. 6–9) is tentative.

Male Secondary Sexual Characters

Aedeagus. The underived condition is assumed to be a short, blunt, open-ended tube, with large, curved, lateral spines. The out-group lacks



FIGS. 2-25. *Euphyes* female genitalia (even numbers—lateral view, odd numbers—ventral view; 2-3, *vestris*; 4-5, *chamuli*; 6-7, *dion*; 8-9, *dukesi*; 10-11, *berryi*; 12-13, *conspicua*; 14-15, *pilatka*; 16-17, *peneia*; 18-19, *singularis*; 20-21, *cornelius*; 22-23, *arpa*; 24-25, *bimacula*. db = ductus bursae, cb = corpus bursae. Scale line = 2 mm.

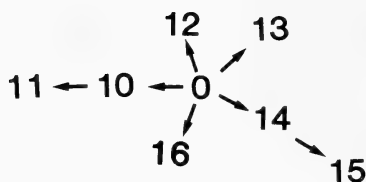


FIG. 26. Hypothesized transformation of male genitalic characters. 0 is plesiomorphic condition. All other numbers are derived and refer to character numbers in text.

cornuti. Figure 26 represents the hypothesized derivation of the following characters:

10. Lateral spines reduced and straight (Figs. 27–29). This condition characterizes the *peneia* group.

11. Lateral spines very small (Fig. 28). This autapomorphy is found in *E. singularis*.

12. Lateral spines absent (Figs. 30–35). This condition is found in the *subferruginea* and *dion* groups. The most parsimonious solution suggests that it has arisen independently in *E. cornelius*.

13. Lateral portion of the aedeagus recurved inward to form a lateral slit-like opening at the posterior end (Figs. 27–29). This condition represents a synapomorphy for the *peneia* group.

14. Cornuti present on the membranous end of the aedeagus (Figs. 30–35). This condition is found in the *subferruginea* and *dion* groups.

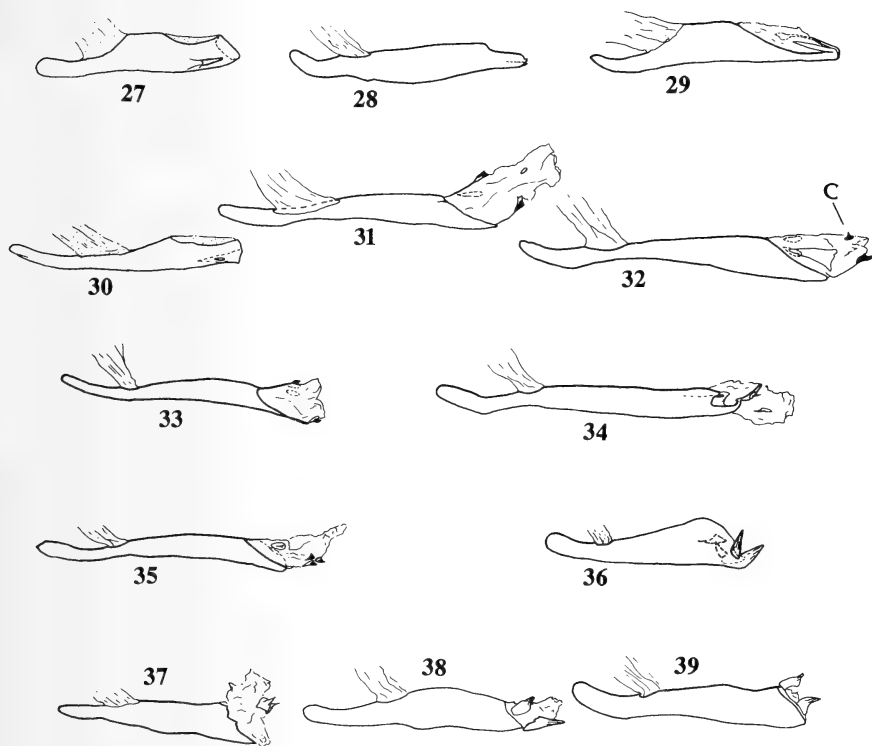
15. Dorsal median cornuti present (Figs. 36–37). This condition is found in *E. vestris* and *E. chamuli*.

16. Lateral spines hinged and flexible (Figs. 36–39). This condition is found in the *vestris* group.

Male stigma. In *Problema* the stigma is absent; in *Arotis* a highly modified stigma is present (Shuey 1987). Consequently, simple out-group comparison does not help determine polarity of this character. The most parsimonious explanation from the phylogenetic analysis indicates that the presence of a stigma represents the plesiomorphic state. Based on other genera in Evans' (1955) group M, the typical hesperiine stigma is relatively slender, the ratio of width to length usually near 1:5 (Figs. 40–45). Burns (1964) speculates that the presence of scent organs in the HesperIIDae may be controlled by a single gene, whereas their development is polygenic. This is consistent with the pattern observed in *Euphyes*.

17. Stigma absent. This condition characterizes the *subferruginea* group.

18. Stigma wide, approximately $\frac{1}{3}$ as wide as it is long (Figs. 46–48). This condition is found in *E. singularis* + *E. cornelius* and *E. conspicua*, and apparently developed independently twice.



FIGS. 27–39. *Euphyes* male genitalia—aedeagus (lateral view): 27, *peneia*; 28, *singularis*; 29, *cornelius*; 30, *subferruginea*; 31, *dion*; 32, *dukesi*; 33, *berryi*; 34, *conspicua*; 35, *pilatka*; 36, *vestris*; 37, *chamuli*; 38, *arpa*; 39, *bimacula*. c = cornuti (the scale of these figures is variable).

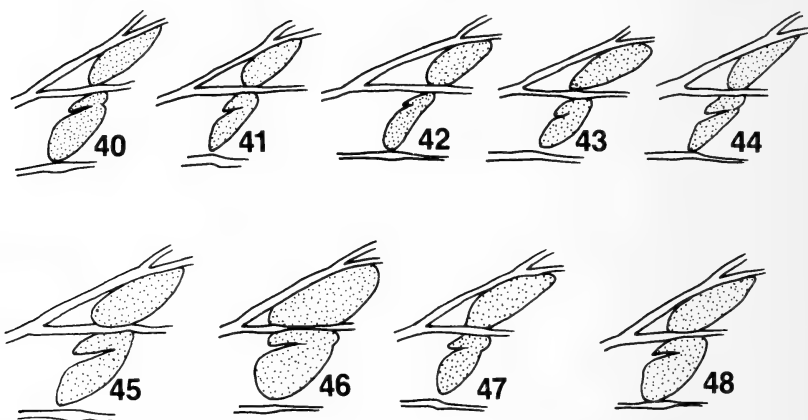
Uncus. In the plesiomorphic condition the two prongs of the uncus are widely separated (Figs. 49–56) and each prong ends posteriorly in a point (Figs. 61–63). The following characters are derived from this condition.

19. Uncus prongs closely spaced (Figs. 57–60). This condition probably arose independently in two lineages, once in *E. arpa*, and again in *E. singularis* + *E. cornelius* + *E. peneia*.

20. Uncus prongs with a small lateral posterior suture (Figs. 61–73). This condition defines *Euphyes*.

21. Uncus prongs posteriorly blunt (Figs. 64–73). This condition is found in the *dion*, *subferruginea* and *vestris* groups.

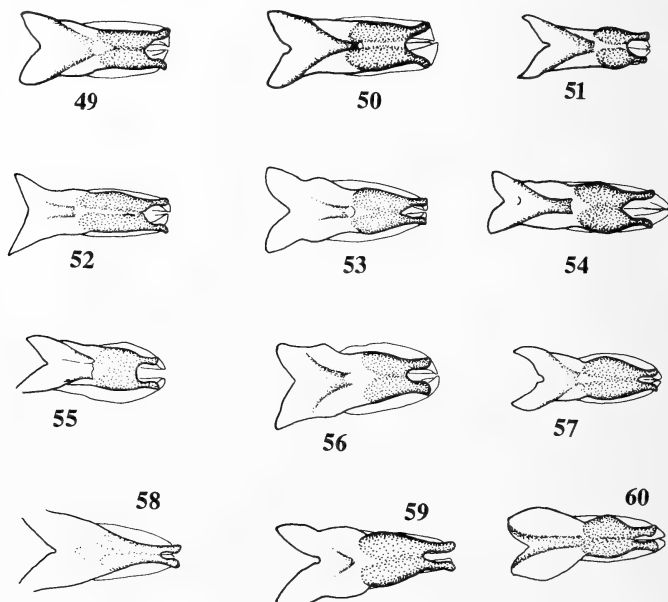
Valva. In the plesiomorphic condition, the valva is short and cup-shaped (Figs. 64–73). This condition is found in the majority of *Euphyes* except for the following two apomorphic conditions.



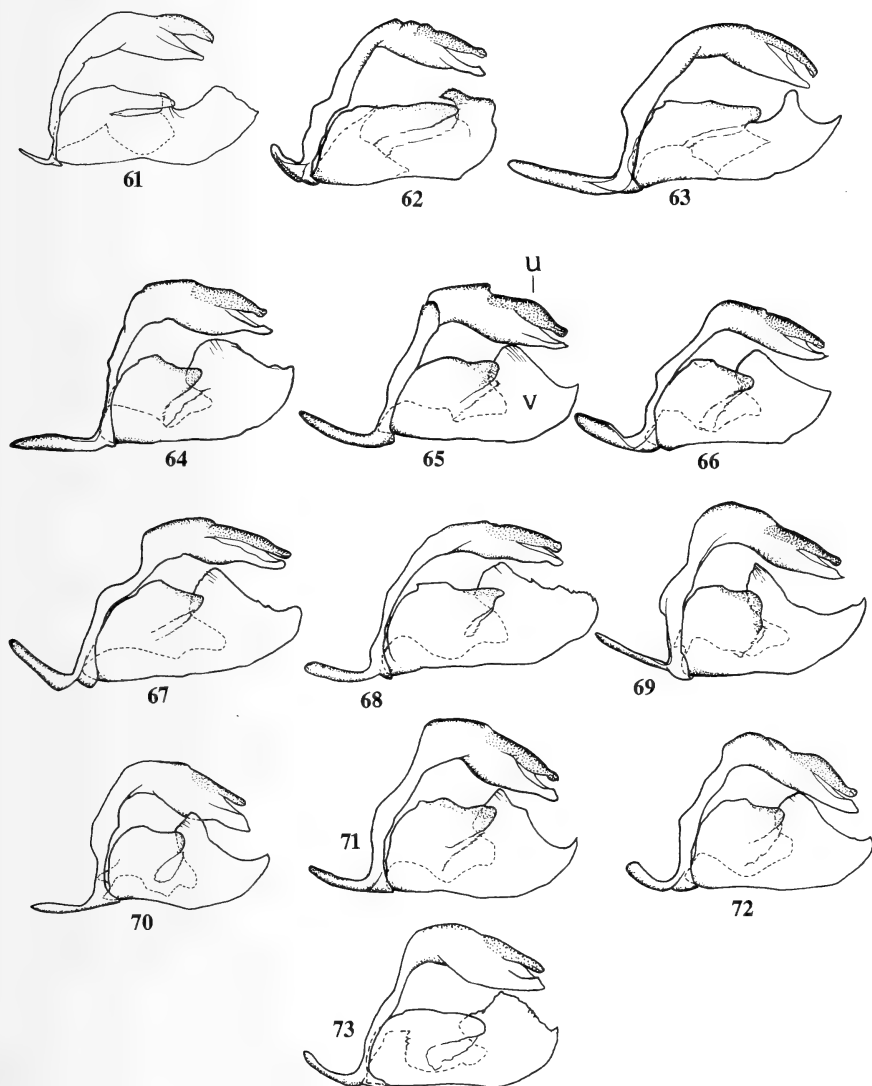
FIGS. 40-48. *Euphyes* male stigmata (dorsal view); 40, *dion*; 41, *berryi*; 42, *bimacula*; 43, *vestris*; 44, *arpa*; 45, *pilatka*; 46, *singularis*; 47, *cornelius*; 48, *conspicua* (the scale of these figures is variable).

22. Valvae basally elongate (Figs. 61-63). This condition is found in *E. peneia*, *E. singularis* and *E. cornelius*.

23. Valvae recurved posteriorly into a hook-shaped spine (Fig. 62). This is an autapomorphy for *E. singularis*.



FIGS. 49-60. *Euphyes* male genitalia—uncus (dorsal view); 49, *dion*; 50, *dukesi*; 51, *conspicua*; 52, *berryi*; 53, *pilatka*; 54, *vestris*; 55, *chamuli*; 56, *bimacula*; 57, *arpa*; 58, *peneia*; 59, *cornelius*; 60, *singularis* (the scale of these figures is variable).



FIGS. 61-73. *Euphyes* male genitalia—valva and uncus (lateral view): **61**, *peneia*; **62**, *singularis*; **63**, *cornelius*; **64**, *dion*; **65**, *dukesi*; **66**, *conspicua*; **67**, *pilatka*; **68**, *berryi*; **69**, *vestris*; **70**, *chamuli*; **71**, *bimacula*; **72**, *arpa*; **73**, *subferruginea*. v = valva, u = uncus (the scale of these figures is variable).

Wing Pattern Characters

Two conditions occur in both the in- and out-groups. The species of *Arotis* are basally black, a condition shared by the *peneia* and *subferruginea* groups and by *E. vestris* and *E. chamuli*. The species of *Prob-*

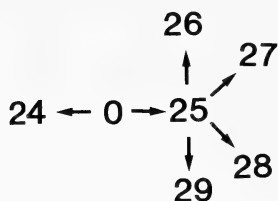


FIG. 74. Hypothesized transformation of wing pattern characters. 0 is plesiomorphic condition. All other numbers are derived and refer to character numbers in text.

lema are tawny with dark wing margins. The ventral hind wings have a light orange medial patch and light orange veins. This pattern is found in the *dion* group and in slightly modified form in *E. bimacula* and *E. arpa*. I originally considered the tawny pattern to be plesiomorphic because of the similarity in pattern between *Problema* and certain members of the *dion* group, especially *E. conspicua*. However, based on the distribution of other characters, the most parsimonious solution suggests that the ancestral wing pattern was black. I hypothesize that the original ancestor of *Euphyes* had black wings; however, it seems likely that this melanic pattern is controlled by one or a few genes which suppress the more complex and presumably polygenically controlled tawny pattern. This could explain why both basic character states of wing pattern of the out-group are found almost unchanged in the in-group. The following conditions are considered apomorphic and the hypothetical derivation of these states is illustrated in Fig. 74. Illustrations of *Euphyes* species can be found in Mielke (1972, 1973), Howe (1975) and Shuey (1988).

24. Tan scales suffused dorsally over otherwise black wing surfaces. This is an autapomorphy for *E. singularis*.

25. Tawny wing pattern. The most parsimonious conclusion is that this condition arose independently twice, once in the *dion* group, and again in *E. bimacula* + *E. arpa*.

26. Orange ray on ventral hind wing. This condition is found in *E. dion*, *E. dukesi*, and *E. bayensis*.

27. Ventral hind wing without an orange patch. This condition apparently arose independently in two lineages, once in *E. pilatka* + *E. berryi* and once in *E. bimacula* + *E. arpa*.

28. Ventral hind wing veins the same color as the wings. This is an autapomorphy for *E. pilatka*.

29. Dorsal tawny areas brown. This is an autapomorphy for *E. dukesi*. The net result of this condition is strikingly similar to that of character 24 when viewed dorsally, but ventral examination reveals that the two conditions occur over the two basic color patterns.

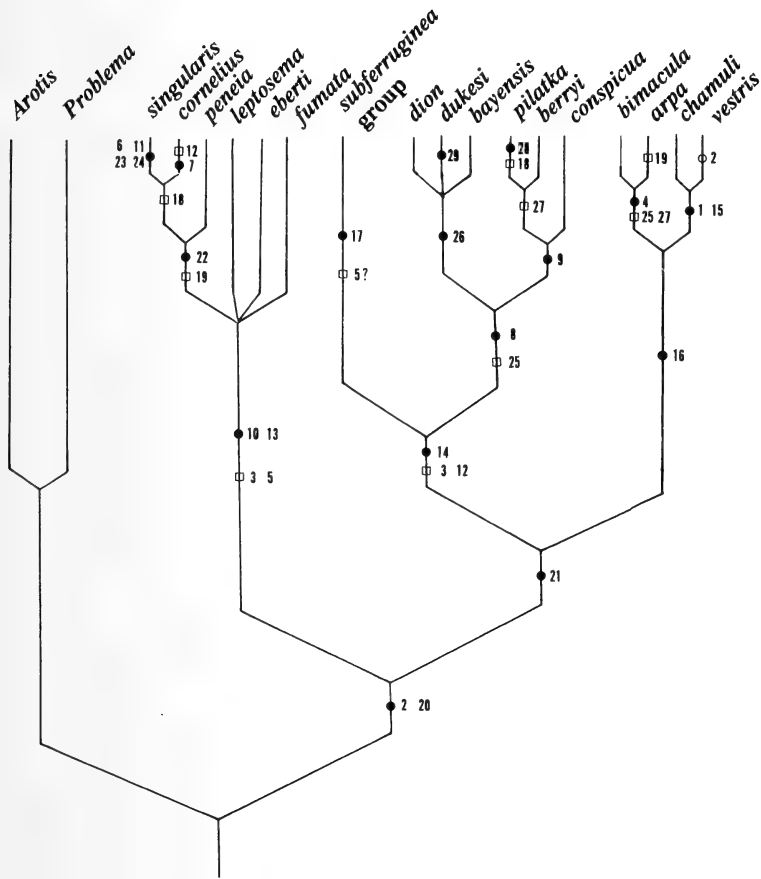


FIG. 75. Hypothesized phylogeny of *Euphyes*. Closed circles are apomorphic characters defining single lineages. Open squares are homoplasic apomorphic characters. Open circle is a reversal. Character numbers refer to character numbers in text. The relationship of *Euphyes* to the out-group genera, *Problema* and *Arotis*, is detailed in Shuey (1987).

PHYLOGENETIC ANALYSIS

The five independent analyses using random seed numbers generated identical cladograms (Fig. 75), which lead me to recognize four monophyletic species groups in *Euphyes*, each characterized by several synapomorphies.

***Peneia* group.** Originally proposed by Mielke (1972), the *peneia* group is defined by lateral fixed spines on the aedeagus (character 10), lateral extensions of the dorsal portion of the ductus bursae (character 5), and black wing pattern. Mielke included four species, *E. peneia*, *E.*

eberti Mielke, *E. leptosema* (Mabille), and *E. fumata* Mielke. I add the two Caribbean species, *E. singularis* and *E. cornelius*, to this group.

Hypothesized relationships within the group are tentative. *Euphyes singularis* and *E. cornelius* are sister species (character 18), which form a monophyletic group with *peneia* (characters 19 and 22). The remaining relations within this clade are unresolved.

Subferruginea group. Mielke (1972) included three species in this group, all of which lack a stigma (character 17): *E. subferruginea*, *E. antra* Evans, and *E. cherra* Evans. Although I examined only one of these species (a male *subferruginea*), Mielke's figures of the male genitalia provided some character states for this analysis. His figures of the female genitalia are more difficult to interpret, but I was able to assign some character states while leaving several states questionable (coded as "?" in data set). The *subferruginea* group shares with the *dion* group the development of cornuti on the aedeagus (character 14), and they are tentatively considered sister groups. If this relationship is correct, the absence of a stigma is a reversal (character 17). *Euphyes ampa* Evans probably belongs in this species group, but Mielke (1972, 1973) did not attempt to place it. Because Mielke's figures are difficult to interpret, *Euphyes ampa* was not included in the phylogenetic analysis.

Dion group. This group is characterized by the doubled-back course of ductus bursae (character 8), thornlike cornuti on the aedeagus (character 14), and tawny wing pattern (character 25). There are two distinct lineages within this group. The first is an unresolved trichotomy defined by presence of an orange ray on the ventral hind wing (character 26) (*E. dion*, *E. dukesi*, and *E. bayensis*). The second lineage is defined by erect corpus bursae (character 9). Within the latter lineage, *E. pilatka* and *E. berryi* are sister species defined by the unmarked ventral hind wing (character 27), and together form the sister group to *E. conspicua*.

Vestris group. This group is characterized by cone-shaped cornuti on the aedeagus (character 16). There are two very distinct group lineages. The first has tawny wings (character 25) and a straight, very elongate corpus bursae (character 4), and includes *E. bimacula* and *E. arpa*. The second lineage includes *E. vestris* and *E. chamuli* and is characterized by black wings, a ductus bursae that lacks sclerotization dorsally (character 1), and by an additional dorsal hinged cone on the aedeagus (character 15).

BIOGEOGRAPHY OF *EUPHYES*

Each species group in *Euphyes* is limited primarily to either tropical America (*subferruginea* and *peneia* groups) or temperate North America (*dion* and *vestris* groups), suggesting that the initial splitting of these

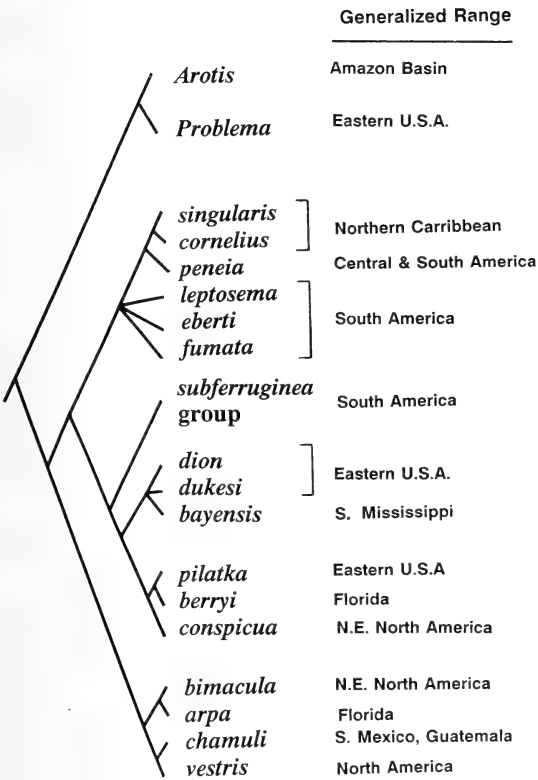


FIG. 76. Hypothesized phylogeny of *Euphyes* as it relates to known species distribution. Ranges derived from material examined, Evans (1955), Mielke (1972, 1973), and Opler and Krizek (1984).

groups is old. The general pattern of distribution of the species groups relative to the hypothesized phylogeny (Fig. 76) does not provide compelling evidence regarding the location of the ancestral species of *Euphyes*. The distribution of these groups suggests that there were two exchanges between North and South America.

The *peneia* group displays the most interesting biogeographic pattern. Three species are essentially confined to the Amazon Basin (*E. eberti*, *E. leptosema*, and *E. fumata*), while *E. peneia* ranges from the Amazon Basin north through central Mexico (Mielke 1972). The sister clade to *E. peneia* (*E. singularis* + *E. cornelius*) occurs in the Caribbean Basin.

There are two competing models for the biogeographic origin of the Caribbean biota. The **dispersal model** has been invoked regularly to explain butterfly distributions in the region (Scott 1972, Brown 1978,

Fontenela & Cruz 1986). This model assumes that Caribbean species represent dispersers from the mainland into previously unoccupied areas. As it applies to the Caribbean basin, all species are presumed to have colonized the islands via over-water dispersal or via land bridges presumably present during the Pleistocene. The most parsimonious dispersal explanation for *Euphyes* distributions is based entirely upon the known current distributions of each species. The first event would have been the immigration of the common ancestor of *E. singularis* + *E. cornelius* onto one of the Greater Antilles, probably Cuba since both species occur there. From there, *E. singularis* apparently immigrated to either Jamaica or Hispaniola, where it differentiated into subspecies *insolata*, and subsequently spread to unoccupied islands. *Euphyes cornelius* may have immigrated from Cuba to the Bahamas where it differentiated into subspecies *agra*.

The **vicariant model** assumes allopatric speciation after barriers separate parts of formerly continuous populations (Rosen 1975, Savage 1982). In the case of the Caribbean Basin, the movement of the Greater Antilles (via plate tectonics) probably provided the vicariance event that transported the common ancestor of *E. singularis* + *E. cornelius* into the area. The islands of Cuba, Puerto Rico, and most of Hispaniola presumably were part of a plate that at one time was either in contact or very near Central America (Buskirk 1985). An additional vicariance event separated Cuba and Hispaniola, and today recognizably different subspecies of *E. singularis* are found on these islands. Because Puerto Rico is on the same plate as is Hispaniola, this model predicts that *E. singularis* may be present but undetected on Puerto Rico. Jamaica and southern Hispaniola have drifted somewhat independently from the other Greater Antilles, and only recently (i.e. within the last 10 million years) has Jamaica approached the other islands. Thus, the vicariant model alone cannot explain the presence of *E. singularis* on Jamaica. Likewise, the presence of *E. cornelius* on the Bahamas is not explained by the model.

A more compelling and realistic explanation combines both models (Fig. 77). The *Euphyes* ancestral species probably arrived in the Caribbean via vicariance (Event 1) where it differentiated into two species lineages. The presence of recognizably different populations of *E. singularis* on Cuba and Hispaniola indicates another vicariant event following the development of that species (Event 2). This is consistent with the geologic history of the area (Buskirk 1985); congruent distribution patterns are found in reptiles (Savage 1982) and fishes (Rosen 1975). Since neither Jamaica (*E. singularis*) or the Bahamas (*E. cornelius*) have contacted either Cuba or Hispaniola respectively, over-water dispersal is probably the most likely explanation for the occur-

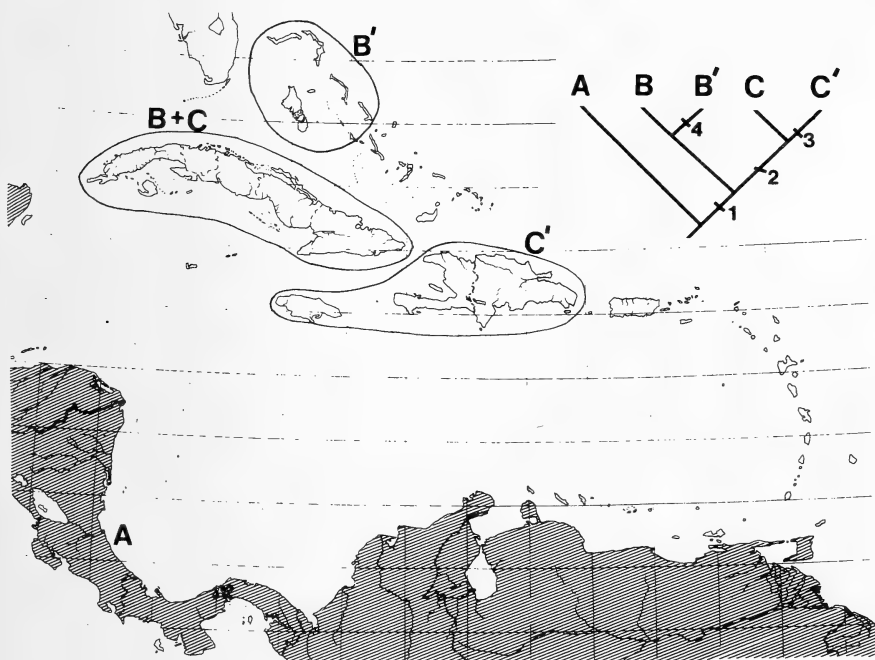


FIG. 77. Area cladogram of the proposed model of *Euphyes* distribution in the Caribbean Basin based on *Euphyes* phylogeny and the tectonic history of the northern Caribbean. See text for explanation of Event numbers on cladogram. A = generalized range of the ancestral species to the *peneia* + *singularis* + *cornelius* lineage. B = range tract of *E. cornelius cornelius*. B' = range tract of *E. cornelius agra*. C = range tract of *E. singularis singularis*. C' = range tract of *E. singularis insolata*.

rence of *Euphyes* on Jamaica and the Bahamas (Events 3 and 4, respectively).

This model for the Caribbean distribution of *Euphyes* is consistent with Miller and Miller's (1990) model for the reconstruction of the West Indian butterfly fauna. They recognize that neither vicariance nor dispersal alone can fully explain the current distribution of butterflies in the Caribbean Basin. Based on their model the initial vicariant event in the Caribbean Basin (Event 1) probably dates to the formation of the proto-Greater Antilles during the late Cretaceous to Eocene periods. The vicariant event which led to differentiation of *E. singularis* on Cuba and Hispaniola (Event 2) may date to the Oligocene to Pliocene period. The dispersal events cannot be dated (Events 3 and 4).

The biogeography of the *subferruginea* group is less complex. All of the known species occur in South America (Mielke 1972).

The *dion* group is restricted to eastern North America. The species are mostly associated with wetlands, and the distribution of these fea-

tures along the Atlantic and Gulf coasts, the Mississippi River drainage, and in glaciated regions may account for the limited ranges of the species in this group. Shapiro (1971) suggested that the present distribution of many wetland butterflies in the eastern U.S. is the result of the happenstance location of refugia during periods of glacial maxima. This may have severely limited the available routes for dispersal into newly formed habitats as they become available behind retreating glaciers.

In addition, several species in the *dion* group have undergone differentiation at the periphery of their ranges. Populations of *E. pilatka* in the Florida Keys have recently been recognized as subspecies *klotsi* (Miller et al. 1985). These populations may have colonized the Keys during a glacial maximum period, when sea levels were lower providing an overland dispersal route into the Keys. Current sea level isolates the Keys as islands, limiting the potential for gene flow with mainland populations. Likewise, *E. conspicua* has recognizable subspecies at the northern and western edges of its range [*orono* (Scudder) and *bucholzi* (Ehrlich & Gillham), respectively]. *Euphyes bayensis* is a subtly differentiated species inhabiting the extreme southern edge of its probable sister species, *E. dion* (Shuey 1988). Although the total range of *E. bayensis* is unknown, its apparent restriction to tidally influenced freshwater marshes (*sensu* Mitsch & Gosselink 1986) suggests that it will be limited to the southern edge of the North American Coastal Plain. Populations of *E. dukesi* from Florida represent an undescribed subspecies (Shuey, unpubl.). This taxon is ecologically similar to mainland *E. dukesi* populations but is morphologically distinct.

This general trend of differentiation at the edge of species ranges in the *dion* group is consistent with allopatric divergence. In these cases, this process may be enhanced by glacial cycling, which results in the expansion and contraction of coastal and inland wetlands on a regular basis (Pielou 1992). This rearrangement of wetland habitat during each glacial cycle presumably fragmented and relocated (via dispersal) populations of wetland butterflies, possibly to small refugia where they may have been more susceptible to environmentally induced or somewhat random genetic changes (Shuey 1985).

Distributions of the two clades of the *vestris* group also suggest allopatric speciation. *Euphyes vestris* is widely distributed throughout North America and northern Mexico. *Euphyes chamuli* occurs to the south of *E. vestris*. Known from less than 10 specimens, *E. chamuli* appears to be confined to the highland region along the Mexican-Guatemalan border. These two species are morphologically very similar and it seems likely that *E. chamuli* is directly derived from a peripheral *E. vestris* population. In addition, isolated populations of *E. vestris* in

southern California (subspecies *harbisoni* Brown & McGuire) are amply distinct from the remaining populations (Brown & McGuire 1983), possibly indicating that *E. vestris harbisoni* represents a relict series of populations with a long history of isolation.

The remaining clade demonstrates a similar pattern. *Euphyes bimacula* occurs in the Great Lakes region of North America and along the Atlantic Coastal Plain south to Georgia. *Euphyes arpa* has been reported from southern Georgia through peninsular Florida (Opler & Krizek 1984). This allopatry could be interpreted as the result of competitive interactions between the sister species. However, *E. arpa* and *E. bimacula* have very dissimilar ecologies, and *E. arpa* is the only *Euphyes* known to use a non-sedge larval food plant: *Serenoa repens* (Bartram) (Palmae), a common plant of xeric habitats in Florida, is the only documented host for *E. arpa* (Opler & Kruzek 1984). *Euphyes bimacula* is more typical of the genus and uses wetland species of *Carex* (Cyperaceae) as the larval food plant. Thus, competition for larval resources is not apparent, and this pattern suggests an ancient allopatric divergence of a formerly widespread ancestral species.

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EFFECT OF SUGAR TYPE ON FOOD INTAKE AND LIPID
DYNAMICS IN ADULT *AGRAULIS VANILLAE* L.
(NYMPHALIDAE)

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ABSTRACT. Newly emerged, laboratory-reared adults of *Agraulis vanillae* L. were tested for feeding response to artificial nectars containing either glucose, fructose, or sucrose. Daily meal size and mass change (particularly lipids) over a five-day period (three of which were feeding days) were compared among individuals feeding on different sugars. Butterflies fed sucrose or fructose ingested significantly larger meals in the first two days of feeding than did individuals fed glucose. Total intake over the three-day experimental period was also significantly greater in sucrose- and fructose-fed individuals. Fructose- and sucrose-fed individuals did not differ from each other in total intake. Sucrose- and fructose-fed individuals differed in mass change and lipid change from individuals fed glucose or not fed at all. Individuals on sucrose and fructose diets increased in mass, and accumulated or lost little lipid, while those on glucose or no adult food lost significant amounts of total mass, lipid mass, and lean mass. Individuals on glucose diets appeared more efficient in maintaining lipid reserves per unit energy ingested than did those in the sucrose and fructose groups. Results are discussed with respect to sugar composition of butterfly-pollinated flowers, foraging energetics, and carbohydrate metabolism.

Additional key words: nectar, sugars, meal size, adult feeding.

There are consistent relations between presence and concentrations of a variety of nectar constituents, including sugars and amino acids, and the type of animal the nectar is intended to attract (Watt et al. 1974, Baker & Baker 1975, 1979, 1982, 1983, Lanza 1988). Flowers pollinated by hummingbirds and hawkmoths produce nectars high in oligosaccharides; this is thought to be related to the high energy demands of these animals (Hainsworth & Wolf 1976, Stiles 1976). However, butterfly flowers are also generally rich in sucrose (but not always; see Watt et al. 1974), though butterflies as a group are thought to have relatively low energy demands (Heinrich 1975). Further, given a choice between nectars containing sucrose, fructose, or glucose, some butterflies show a clear preference for sucrose nectars over glucose nectars (Ehrhardt 1991, 1992).

Although there is great diversity in the importance of food intake among adult lepidopterans relative to reserves from larval feeding (Boggs 1986, May 1992), studies of food intake among nectar-feeding lepidopterans generally have shown that carbohydrates in the diet significantly increase female fecundity (e.g., Stern & Smith 1960, Murphy et al. 1983, Leather 1984, Carroll & Quiring 1992). Lepidopterans that require nectar as adults therefore should evolve preferences for those carbohydrates that are most effective at increasing fecundity or other fitness components (Pyke 1984).

In this study, I examine effects of sugar type (sucrose, fructose, or glucose) on adult food intake and accumulation of lipid reserves in *Agraulis vanillae* L., which is an avid flower visitor. I asked three main questions:

a) Do these butterflies respond differently to artificial nectars of the three sugar types equal in concentration and therefore in total energy content?

b) Do diets composed of different sugar types influence the rate at which metabolic reserves, particularly lipids, are stored or exhausted?

c) Do adults compensate for low emergence weights by greater adult food intake to supplement lower metabolic reserves from larval feeding, as suggested by Boggs (1981) and May (1992)?

METHODS AND MATERIALS

The gulf fritillary, *Agraulis vanillae* L. (Nymphalidae), is a heliconiine butterfly that frequents a variety of open and disturbed habitats in Florida, from about mid-May until November. It typically is found near its larval food plant, *Passiflora incarnata* L. (Passifloraceae). Oviposition occurs throughout the flight season, eggs are laid singly on host plants or on nearby vegetation, and there are multiple, overlapping generations per year. Most females are reproductively mature and capable of ovipositing within 12–18 hours after emergence (Arbogast 1965). Large-scale southerly migrations take place from late August through November (Walker 1978), although little is known of the destination and overwintering biology of the migrants. Adult longevity is from 2–3 weeks (Arbogast 1965, May, unpubl. data). Food habits of adults in the field and their effects on lipid reserves have been studied extensively (May 1992).

Third through fifth instar larvae were collected during summer 1990 from several populations in the DeLand, Florida area (29°06' latitude, 81°22' longitude) and taken to the laboratory for rearing. Larvae were fed in the laboratory with field-collected foliage of *Passiflora incarnata*, and were maintained at ambient photoperiod and heated for 12 hours a day to 28–30°C. Nighttime temperatures were approximately 26°C. Pupae were maintained under similar conditions, and upon adult emergence, I allowed each individual to expel meconial wastes before determining sex, wet mass, and forewing length. Wet mass was determined by weighing freshly emerged individuals in tared glassine envelopes. Butterflies were assigned to feeding treatment on the basis of emergence order in a repeating sequence of fructose, glucose, and sucrose (the first adult was fed fructose, the second glucose, the third sucrose, the fourth fructose, and so on). In addition, several adults with split or otherwise

nonfunctional probosces were maintained without food under the same conditions as the feeding butterflies for comparison. However, as these individuals were not randomly assigned to treatment, they were excluded from statistical analyses.

After postemergence data were collected, each butterfly was marked and placed in a $60 \times 60 \times 70$ cm screened flight cage exposed to the same environmental conditions as the larvae and pupae. Beginning on the day after emergence, individuals were fed to satiation once a day on a 31% (weight/weight) aqueous solution of either sucrose, fructose, or glucose. Flowers visited by *Agraulis* range from 18–40% sucrose equivalents (May 1992); 31% was chosen somewhat arbitrarily within this range. Sugar solutions were heated to approximately 28°C before feeding trials began. The insects were fed from microcapillary tubes containing the appropriate sugar solution using the procedure described by May (1985). An individual was considered satiated after withdrawing its proboscis from the microcapillary tube three times. Volume of nectar consumed was recorded for three consecutive days, and on the fifth day after emergence each individual was weighed and frozen for lipid extraction.

Before lipid extraction, individual butterflies were dried to constant mass in a drying oven at approximately 50–60°C and weighed within 30 minutes after removal from the drying oven. Lipid extraction followed the technique of Brower (1985). Each butterfly was homogenized in a centrifuge tube with 10 ml of petroleum ether, then vortexed and placed in a shaking water bath at 35°C for 30 minutes, with vortexing every 10 minutes. Solids were allowed to settle for 30 minutes, and the supernatant was withdrawn with a Pasteur pipet and transferred to a preweighed aluminum pan on a 30°C hot plate. The remaining solids were extracted again with an additional 15 ml of petroleum ether, vortexed and the procedure was repeated. Weighing pans with supernatant were allowed to evaporate overnight in a fume hood, and the remaining lipids were weighed. Lean mass was calculated as dry mass minus lipid mass.

To estimate changes in lipid stores over the course of the experiment, I estimated emergence lipid reserves using the regression of final wet mass vs. lipid mass of all individuals at the end of the experiment, assuming that the same relationship held for individuals at emergence. Regressions for males and females gave identical equations ($y = 0.07x - 0.003$, where y is lipid mass and x is final wet mass; $F = 30.66$, $P = 0.0001$ for females, $F = 12.35$, $P = 0.003$ for males). Emergence lipid mass was estimated by substituting emergence wet mass for final wet mass in this regression. For example, a butterfly weighing 250 mg at emergence would be estimated to have an emergence lipid mass of

TABLE 1. Meal sizes of *Agraulis vanillae* adults fed different sugars. Figures indicate mean \pm SE; sample size in parentheses.

Meal volume (μ L)	Treatment		
	Sucrose	Fructose	Glucose
Day 1	88.7 \pm 7.2 (14)	83.2 \pm 6.5 (15)	25.6 \pm 3.7 (16)
Day 2	56.7 \pm 6.5 (14)	58.0 \pm 5.5 (15)	29.6 \pm 3.3 (15)
Day 3	44.4 \pm 7.5 (13)	36.1 \pm 5.4 (15)	28.6 \pm 4.8 (15)
Total	189.8 \pm 18.7 (13)	177.3 \pm 9.8 (15)	83.8 \pm 9.6 (15)

0.07 \times 250 = 0.003 mg of lipid (17.5 mg). Change in lipid mass was calculated as estimated emergence lipid mass - final lipid mass.

I calculated two values, one intended to indicate the relations between energy ingested and the amount of lipid stored, and the other an estimate of total energy expenditure. The first, labeled Energy Use Ratio (stored energy/ingested energy), is the ratio between energy remaining as stored lipid at the end of the experiment (calculated as lipid mass (μ g) \times 0.039J/ μ g [from Schmidt-Nielsen 1975]) and energy ingested in the adult diet (calculated as total volume consumed (μ L) \times 5.78J/ μ L [see Bolten et al. 1979 for details of calculation]). This figure should indicate how efficiently the butterflies use ingested energy and convert it to lipid reserves. The second estimate, Total Energy Expenditure, is calculated as energy intake by the adult plus energy released from lipid metabolism (estimated as change in lipid mass multiplied by the energy content of lipid, as explained above). This latter estimate is a rough approximation at best, due to estimation errors introduced by using the regression described above to estimate emergence lipid reserves.

RESULTS

The type of sugar present in artificial nectars significantly affected meal size, and subsequently affected the size of lipid reserves. Butterflies fed longer on sucrose and fructose nectars than glucose nectar (Table 1). Two-way analyses of variance (ANOVAs) using sugar type and sex of the butterfly as classifying variables showed no significant effects of sex or interactions between sex and diet among variables, so male and female data were combined and analyzed with one-way ANOVAs. These analyses showed significant effects of sugar type on day 1, day 2, and total volumes (respectively, $F = 36.3$, $P = 0.0001$; $F = 9.5$, $P = 0.0004$; $F = 20.2$, $P = 0.0001$). Meal volume on day 3 did not differ significantly among groups ($F = 1.8$, $P = 0.186$). For the three variables that showed significant differences, multiple comparison tests (Scheffe's F-test) showed that sucrose and fructose meal volumes did not differ significantly (at the 0.05 level), but both were significantly greater than glucose meal volumes.

TABLE 2. Body size and composition characteristics of *Agraulis vanillae* adults fed different sugars. Figures indicate mean \pm SE; sample size in parentheses.

	Treatment			
	Sucrose	Fructose	Glucose	No food
Final wet mass (mg)				
Male	245 \pm 34 (3)	274 \pm 8 (7)	187 \pm 10 (5)	119 (1)
Female	330 \pm 24 (9)	322 \pm 29 (7)	252 \pm 13 (11)	215 \pm 34 (4)
Final dry mass				
Male	92 \pm 14 (3)	105 \pm 3 (7)	77 \pm 6 (5)	47 (1)
Female	124 \pm 9 (10)	108 \pm 6 (7)	95 \pm 4 (11)	84 \pm 11 (4)
Lipid mass				
Male	13 \pm 5 (3)	15 \pm 2 (7)	11 \pm 2 (5)	6 (1)
Female	24 \pm 3 (10)	16 \pm 2 (7)	14 \pm 2 (11)	11 \pm 3 (4)
Lean mass				
Male	79 \pm 10 (3)	90 \pm 3 (8)	66 \pm 5 (5)	41 (1)
Female	101 \pm 6 (10)	92 \pm 4 (7)	81 \pm 3 (11)	73 \pm 8 (4)
Mass change				
Male	12 \pm 15 (3)	23 \pm 10 (7)	-73 \pm 22 (5)	-142 (1)
Female	7 \pm 20 (9)	8 \pm 35 (7)	-66 \pm 16 (11)	-97 \pm 8 (4)
% Lipid (of dry mass)				
	17.3 \pm 1.1 (13)	14.6 \pm 0.9 (15)	14.1 \pm 1.0 (16)	12.7 \pm 2.0 (5)

Differences in meal sizes due to sugar type significantly affected changes in weight and lipid storage among the treatment groups (Table 2). Although females are capable of oviposition within one day after emergence (Arbogast 1965), no oviposition occurred among caged females during the experiment, so any resources allocated to egg development are reflected in the body masses determined for females. Two-way ANOVAs of emergence weight and forewing lengths, using sex and treatment as classifying variables, showed significant sexual differences in body size (females are larger in linear dimensions and mass at emergence), but no significant differences in starting conditions among treatments (Table 3). Thus, changes in body size and composition measured on the fifth day (after three days of feeding) can be attributed to the effects of the different sugars on feeding and mass accumulation or depletion. Two-way ANOVAs using sex and treatment as the classifying variables showed that wet mass, dry mass, and lean mass at the end of the experiment varied significantly among treatments and between sexes (Table 3). Mass change varied significantly among treatments, but not between sexes. Lipid mass varied significantly between sexes, but differences among treatments were slightly above the level of significance ($P = 0.08$). Percent lipid (of dry mass) did not vary significantly among treatments or sexes; the data in Table 3 are for

TABLE 3. Results of 2-way ANOVA's of body composition characteristics. Statistical significance indicated by bold type.

Variable	Effect of		
	Treatment	Sex	Interaction
Emergence mass	F = 0.176 P = 0.839	F = 8.817 P = 0.005	F = 0.009 P = 0.991
Forewing length	F = 0.407 P = 0.668	F = 3.487 P = 0.068	F = 1.101 P = 0.341
Final wet mass	F = 7.989 P = 0.001	F = 12.72 P = 0.001	F = 0.311 P = 0.734
Dry mass	F = 5.698 P = 0.007	F = 8.229 P = 0.007	F = 1.876 P = 0.167
Lipid mass	F = 2.636 P = 0.085	F = 5.454 P = 0.025	F = 1.826 P = 0.175
Lean mass	F = 6.973 P = 0.003	F = 8.466 P = 0.006	F = 1.811 P = 0.177
Mass change	F = 8.608 P = 0.001	F = 0.044 P = 0.834	F = 0.105 P = 0.900
% Lipid (of dry mass)	F = 0.661 P = 0.522	F = 2.672 P = 0.110	F = 1.635 P = 0.208

pooled sexes. Butterflies on fructose and sucrose diets added mass during the experimental period, and this was partially due to accumulation of lipids in the sucrose group, whereas individuals fed glucose or nothing lost mass and apparently depleted metabolic reserves present at emergence. The greatest mass loss was in the nonfed butterflies (Table 2); these data, however, were not statistically analyzed with the other treatment groups.

Estimated changes in lipid stores (Table 4) should be interpreted with caution because of estimation errors in emergence lipid masses introduced by the use of regression as described above. Standard errors in Table 4 reflect only variance in the lipids actually measured at the end of the experimental period; estimation errors from calculation of emergence lipid mass were not carried through to these figures. Two-way ANOVAs showed no significant differences among treatments in estimated emergence lipid weights ($F = 0.176$, $P = 0.839$), although females had significantly more lipid ($F = 8.8$, $P = 0.005$). Lipid change did not differ significantly among treatments ($F = 3.025$, $P = 0.06$), although the probability level is close. There was no difference in lipid change between sexes ($F = 0.03$, $P = 0.865$). According to these estimates, individuals on sucrose accumulated fat, those on fructose lost a small amount, and those on glucose or no food lost more lipid. Multiple comparison tests (Fisher PLSD) showed that significant differences existed between the sucrose and glucose treatments, between fructose and glucose treatments, but not between sucrose- and fructose-fed butterflies.

TABLE 4. Lipid mass and energy utilization as a function of treatment in *Agraulis vanillae*. Figures indicate mean \pm SE; sample size in parentheses. N/A = not applicable.

	Treatment			
	Sucrose	Fructose	Glucose	Not fed
Initial lipid (mg)	17 \pm 1 (17)	17 \pm 2 (17)	18 \pm 1 (18)	17 \pm 1 (8)
Lipid change (mg)	-3 \pm 2 (13)	1 \pm 1 (15)	5 \pm 2 (15)	8 \pm 2 (5)
Energy use ratio	0.80 \pm 0.11 (13)	0.62 \pm 0.06 (15)	1.40 \pm 0.30 (15)	N/A
Total energy use (J)	974 \pm 66 (13)	1060 \pm 53 (15)	657 \pm 69 (15)	307 \pm 85 (5)

Energy Use Ratio and Total Energy Expenditure differed significantly among treatments (Table 4). Two-way ANOVAs of these indices used treatment and sex as classifying variables, and excluded individuals that did not feed. Both indices showed significant differences among treatments, but not between sexes (Use ratio: $F_{\text{treat}} = 9.3$, $P = 0.0005$, $F_{\text{sex}} = 0.407$, $P = 0.53$; Expenditure: $F_{\text{treat}} = 12.19$, $P = 0.0001$, $F_{\text{sex}} = 0.20$, $P = 0.655$). Multiple comparison tests (Fisher PLSD) showed for both that the sucrose and fructose groups differed significantly from the glucose group but not from each other ($P < 0.05$). These estimates suggest that a) per unit of energy ingested as an adult, the butterflies fed glucose had relatively greater amounts of energy stored as lipid at the end of the experiment than did individuals in the fructose and sucrose groups, and b) the glucose-fed individuals had significantly lower total energy budgets than did the fructose- and sucrose-fed individuals.

As a test of the hypothesis that individuals with low emergence weights (and therefore low lipid reserves; correlation between emergence weight and lipid weight for pooled sexes, $r = 0.70$, $df = 18$, $P < 0.01$) ingest more food to supplement lipid reserves from larval feeding, I sought correlations between forewing length or emergence weight and volume of nectar imbibed on each day of the feeding trial as well as total volume imbibed. If correct, this hypothesis would predict a negative correlation between emergence weight and the volume of nectar taken. Because many correlations were performed in this analysis, I used the Systat software package (Systat, Inc., Evanston, Indiana) and a sequential Bonferroni technique (Rice 1989) to ensure that the probability of type I error was less than 0.05 for all correlations. Considering both individuals within treatment groups and all treatments pooled together, no consistent relations between body size and nectar consumption were found (Table 5). Although most correlations were not significant, the nature of the body size vs. volume consumed relationship differed among treatments, and between days within some treatments. Body size indicators and volume consumed were negatively correlated in some cases, though never significantly, and positively in

TABLE 5. Correlation coefficients between body size traits and nectar consumption. Correlations significant at the 0.05 level are in bold type.

Nectar consumption	Body size trait, by treatment							
	Sucrose		Fructose		Glucose		All treatments	
	Wt.*	FW**	Wt.	FW	Wt.	FW	Wt.	FW
Day 1	0.227	0.319	-0.207	0.232	-0.498	-0.051	-0.077	0.284
Day 2	0.209	0.537	-0.036	-0.106	-0.242	0.374	0.032	0.277
Day 3	0.190	0.428	0.311	0.278	0.081	0.224	0.149	0.352
Total	0.372	0.664	0.037	0.620	-0.359	0.053	0.023	0.431

* Wet weight at emergence.

** Forewing length.

others. The only significant correlation coefficient was opposite of what was predicted, i.e., butterflies with larger forewings consumed more nectar over the three-day feeding period in the fructose group.

DISCUSSION

Type of sugar present in nectar clearly affects feeding behavior and lipid dynamics in *Agraulis vanillae*, although the reason for this difference is not obvious. All three sugar solutions had equal sugar concentrations, and therefore equal absolute energy content per unit volume. Based on energy content alone, there is no adaptive reason to expect butterflies to prefer one sugar type over another, unless there are differences in metabolizable energy between sugar types. Further, the difference is not between monosaccharides and oligosaccharides, as responses to sucrose and fructose nectars were not significantly different in any of the measures examined, while both differed significantly from the response to glucose. Fructose and sucrose clearly are preferred by this butterfly as judged by average meal size. The sugar types also differed with respect to changes in daily meal size; this decreased from day 1 to 3 with sucrose and fructose nectars, but stayed constant in glucose-fed butterflies.

These differences in meal size and thus energy intake among treatments significantly affected body composition in five-day old adults. Sucrose- and fructose-fed butterflies had larger total mass and lean mass than glucose-fed butterflies. Although differences in lipid contents were not statistically significant, it is likely that differences in lipid storage account for some of the differences in mass change. Sucrose- and fructose-fed butterflies either accumulated lipids or depleted very little, while glucose- and nonfed butterflies depleted lipids. Lean-mass loss among these latter groups suggests these butterflies were metabolizing nonlipid body constituents as well.

The proportion of body mass allocated to lipid did not differ signif-

icantly among groups, suggesting that as butterflies metabolize lipid stores, they also metabolize a relatively constant proportion of nonlipid components, and that this is independent of sugar type in the adult diet. The differences seen in the indices of energy use derived here may be due to either a) physiological differences in sugar metabolism among sugar types (glucose-fed butterflies showed greater lipid reserves per unit of energy ingested) or more likely, b) dietary differences lead to behavioral differences in adult butterflies, with glucose-fed butterflies showing lower activity levels and therefore conserving stored lipids that are not replaced by adult dietary intake.

These findings are especially puzzling in light of the traditional view of insect carbohydrate metabolism, which holds that the primary sugar circulating in the hemolymph is trehalose, a disaccharide synthesized from glucose in a process that is apparently relatively expensive metabolically (Chapman 1979). Trehalose is presumably the carbohydrate that is the intermediate between ingested sugars and lipid storage in the fat body. Thus, ingested sucrose and fructose first must be modified to glucose and then trehalose, which would suggest that given equal-concentration solutions of glucose, sucrose, and fructose, glucose should be the most efficient in terms of conversion to trehalose. Other butterflies studied can metabolize all three of the sugars via carbohydrases (Watt et al. 1974, Ehrhardt 1991).

In light of the field foraging behavior of *Agraulis vanillae*, the results here are consistent with their failure to discriminate among flowers differing in energy content in natural situations. Given a choice between flowers of significantly different energy contents, they often fail to preferentially visit flowers with the highest energy contents, whereas another species (*Phoebis sennae* L., Pieridae) does selectively visit flowers with higher energy content (May 1992). In addition, there may be little selective pressure for butterflies to discriminate flowers on the basis of sugars, as it may be rare for flowers to produce nectars with only one type of sugar. For example, Baker and Baker (1983) found that in a sample of 765 nectars from a variety of pollination syndromes tested for sugar content, only nine had one type of sugar only. Seven nectars had sucrose only, two had glucose only, and none had fructose only. As most nectars apparently have some combination of all three sugars (649 in the Bakers' sample), butterflies may respond to relative sweetness or detectability, which is higher for sucrose and fructose than glucose.

These butterflies showed no clear relationship between emergence weight and amount of food taken by adults. The best indicator of fat reserves at eclosion, the emergence wet weight, showed no significant correlations with any measure of nectar consumption. These data thus

provide no support for the hypothesis that variation in adult feeding by this species can compensate for poor larval conditions by increasing adult intake in individuals with low metabolic reserves at emergence (May 1992), although the feeding opportunities available in this laboratory context are drastically different from feeding opportunities available to wild butterflies.

Whatever the reasons for the effect of different sugars on adult intake, these results are generally in accord with studies of nectar composition in butterfly-visited flowers, which are typically sucrose-rich (Baker & Baker 1975, 1979, 1982, 1983). Watt et al. (1974), however, showed that some *Colias* species (Pieridae) preferred flowers that have high proportions of glucose and fructose. Recent experimental studies of nectar preference by the butterfly *Battus philenor* L. (Papilionidae) showed a clear preference for sucrose and fructose over glucose, and a less dramatic preference for sucrose over fructose (Ehrhardt 1991, 1992). Sucrose-rich nectars have been suggested by other workers to be associated with high energy-demand pollinators such as hummingbirds (Hainsworth & Wolf 1976, Stiles 1976). Relative to most other pollinator groups, however, butterflies are probably one of the pollinator groups with the lowest energy demands, based on flight energetics (Heinrich 1975, Zebe 1954) and low nectar volumes in butterfly-visited flowers (Watt 1974, May 1988, 1992).

The differences among feeding response to different sugars seen here are also consistent with studies of sugar sensitivity and preference in some flies and orthopterans, which can detect sucrose at very low concentrations, fructose at slightly higher concentrations, and glucose only at much higher concentrations (Hansen 1978, Cook 1977). Ehrhardt (1991) suggests that these abilities and preferences may be general in insects.

Some caution needs to be exercised in interpreting these feeding differences in the context of foraging behavior in natural situations, as butterflies rarely if ever have the opportunity to feed uninterruptedly to satiation from a single source. However, the marked differences in responses to different types of sugars suggest that more detailed studies of sugar preferences and metabolism in a variety of insects might be fruitful.

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CLINAL VARIATION IN *HESPERIA LEONARDUS* (HESPERIIDAE) IN THE LOESS HILLS OF THE MISSOURI RIVER VALLEY

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ABSTRACT. Specimens of *Hesperia leonardus* Harris were collected from a potential subspecies intergrade area known as the Loess Hills, which are bluffs of xeric prairie extending from the southeastern tip of South Dakota to the northwestern corner of Missouri. Specimens were rated for five characteristics: (1) forewing length, (2) ventral hindwing color, (3) ventral hindwing median band size, (4) dorsal fulvousness of males, and (5) transparency of the dorsal forewing hyaline spot in females. Reference specimens included typical *H. l. pawnee* Dodge and typical Ozark *H. l. leonardus*. Comparisons by three multivariate statistical procedures showed that the specimens formed a complete cline of characteristics between *H. l. leonardus* and *H. l. pawnee* within several Iowa counties. All three analyses support north to south gradations from *H. l. pawnee* to *H. l. leonardus*, with populations in Monona, Harrison, and Pottawattamie counties in Iowa representing the greatest amount of intergradation. Results from this study support previous conclusions that *H. l. leonardus* and *H. l. pawnee* are conspecific.

Additional key words: intergrade, skipper, multivariate analysis, prairie, Iowa.

The Loess Hills are a series of loess covered bluffs formed by past action of winds on the Missouri River floodplain, extending approximately from the extreme southeastern corner of South Dakota to northwest Missouri (Fig. 1). The majority of these bluffs occur in Nebraska and Iowa, although by far the most extensive areas are in Iowa. The Loess Hills are composed of xeric, mixed-grass prairie, drought-tolerant forbs, and hardwood [e.g. bur oak (*Quercus macrocarpa* Michx., Fagaceae)] forests, invaded with red cedar (*Juniperus virginiana* L., Cupressaceae). Dominant grasses (Poaceae) include little bluestem (*Andropogon scoparius* Michx.), side-oats grama [*Bouteloua curtipendula* (Michx.) Torr.], and hairy grama (*B. hirsuta* Lag.). Although prairies dominate in the northern hill region, forests dominate in the southern hills, covering all but the driest, most exposed ridgetops and bluffs (Mutel 1989). A number of rare plants and animals reside in the Loess Hills.

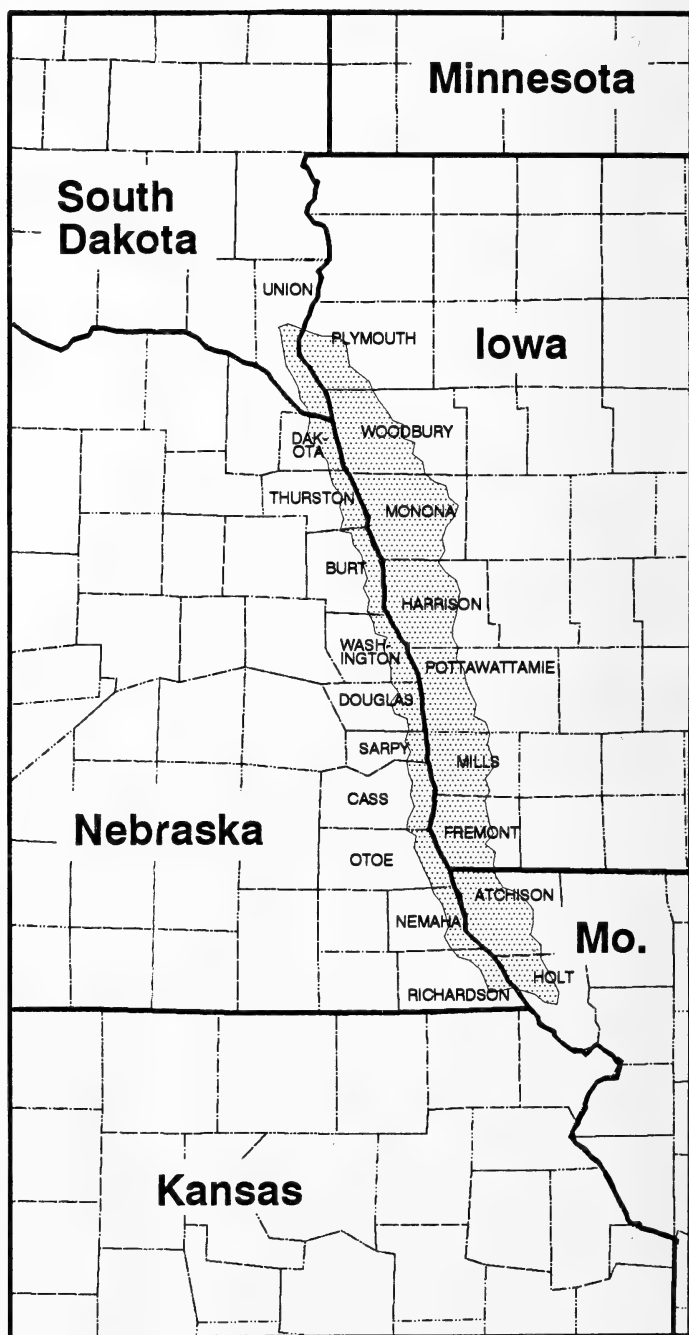


FIG. 1. Generalized geographic location of the Loess Hills.

Scott and Stanford (1981) concluded that Leonard's skipper (*Hesperia leonardus leonardus* Harris) and the pawnee skipper (*Hesperia leonardus pawnee* Dodge) are conspecific based primarily upon a series of intermediates from central Minnesota and a few specimens from adjacent states. Similarities in male genitalia, host plant requirements, and nectar sources between the two taxa also were mentioned. However, some authors still consider the two phenotypes to be distinct species, based on differences in habitat and appearance (Tilden & Smith 1986, Klassen et al. 1989).

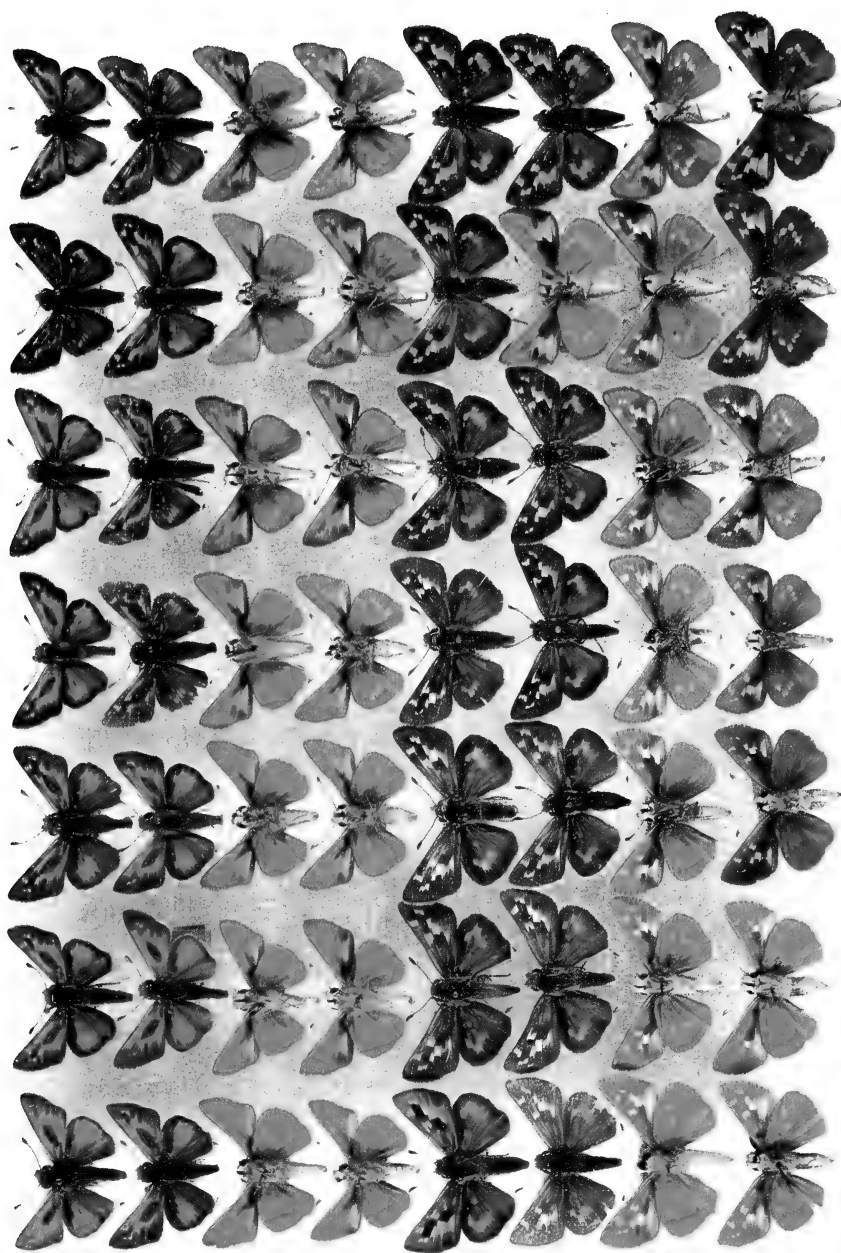
Scott and Stanford (1981) suggested a blend zone between the two phenotypes. This blend zone included areas of southeastern Nebraska and western Iowa, part of which is encompassed by the Loess Hills. Unfortunately, very few specimens of *H. l. leonardus* or *H. l. pawnee* were known from the Loess Hills. Lindsey (1921) reported specimens from Sioux City, Iowa, probably collected in what is now Stone State Park in Plymouth and Woodbury counties, Iowa (W. W. McGuire, pers. comm.). Also, Barber (1894) cited a record of *H. leonardus* (sic *leonardius*) by W. E. Taylor from Nemaha Co., Nebraska that may have originated in the Loess Hills. In 1986, we rediscovered *H. l. pawnee* at Sioux City Prairie, and in 1988 we discovered a new colony in Union Co., South Dakota.

These recent discoveries of *H. l. pawnee* in the Loess Hills prompted us to survey additional sites within the Loess Hills. Our objectives were to (1) document the occurrence of *H. l. leonardus* and/or *H. l. pawnee* within the Loess Hills south of the previously mentioned sites, (2) search for identifiable intermediates that would substantiate the blend zone reported by Scott and Stanford (1981), and (3) record behavioral and ecological observations.

MATERIALS AND METHODS

From 1989 through 1991, we conducted an intensive search of native prairie sites located within the Loess Hills from Union Co., South Dakota to Holt Co., Missouri. Adult *Hesperia* were collected and pertinent behavioral, biological, and ecological information was recorded.

Spread specimens were rated for five characteristics, as used by Scott and Stanford (1981), to distinguish between *H. l. leonardus* and *H. l. pawnee*. These five characteristics were: (1) forewing length, (2) ventral hindwing color [rated from 0 to 7 using eight standard reference specimens varying from golden (males) or greenish golden (females) in *H. l. pawnee* to dark reddish brown in *H. l. leonardus*], (3) ventral hindwing median band size (rated from 0 to 4 using five reference specimens varying from absence of band to large, distinct spots), (4) dorsal lightness of males (rated from 1 to 6 using six reference specimens varying from



light fulvous in *H. l. pawnee* to very dark in *H. l. leonardus*), and (5) transparency of the dorsal forewing hyaline spot in females (rated from 1 to 4 using four reference specimens varying from white in *H. l. pawnee* to dark yellow in *H. l. leonardus*). Reference specimens also included examples of typical *H. l. pawnee* from west-central Nebraska and Pipestone Co., Minnesota, and typical *H. l. leonardus* from the Missouri Ozarks. Reference specimens also were rated for the five variables listed above. Two additional variables used by Scott and Stanford (1981), dorsal lightness of females and darkness of ventral forewing tornus, were not used because they were too variable to be useful for comparative purposes, even among typical *H. l. pawnee* individuals.

We used three multivariate statistical procedures to identify relationships between specimens at different locations (counties). Specific analyses included cluster analysis, canonical discriminant analysis, and discriminant analysis based on the observed variable (SAS Institute 1988). Because classification criteria differed by sex, all analyses were conducted separately for males and females. Cluster analysis, using the average linkage method, was conducted on specimens from both the potential intergrade zone (Loess Hills) and the reference specimens. Canonical discriminant analysis also was used for these (Loess Hills and reference) specimens to provide an alternative procedure for classification. For the final procedure, discriminant analysis, specimens from Union, Plymouth, and Woodbury counties in Iowa were classified as *H. l. pawnee* and those from Mills and Fremont counties in Iowa as *H. l. leonardus*. These were then used as a known data set to discriminate specimens as *H. l. pawnee* or *H. l. leonardus* for all eight Loess Hills counties.

RESULTS AND DISCUSSION

By 1991, we had investigated nearly every Loess Hills county in Nebraska and all Loess Hills counties in South Dakota, Iowa, and Missouri. New populations of *H. l. leonardus/pawnee* were discovered and collected in Monona, Harrison, Pottawattamie, Mills, and Fremont counties in Iowa. No specimens were found in Nebraska or Missouri. A total of 208 Loess Hills specimens, representing 43 sites, was rated. Densities of *H. leonardus* varied between sites, appearing to be influ-

←

FIG. 2. Loess Hills specimens of *Hesperia leonardus*. Column 1 = Union Co., South Dakota; column 2 = Plymouth and Woodbury co.'s, Iowa; column 3 = Monona Co., Iowa; column 4 = Harrison Co., Iowa; column 5 = Pottawattamie Co., Iowa; column 6 = Mills Co., Iowa; column 7 = Fremont Co., Iowa.

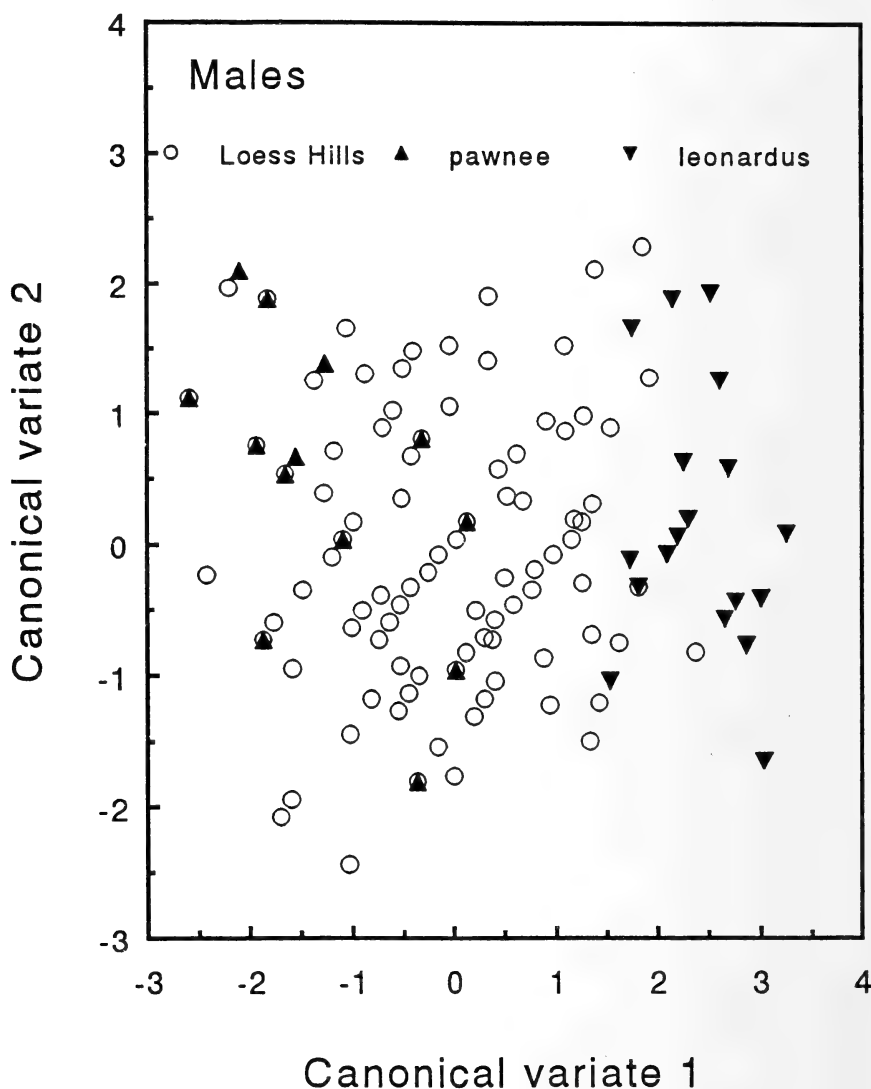


FIG. 3. Results of the canonical discriminant analysis of *Hesperia leonardus* populations—males.

enced most by habitat quality and availability of blazing star (*Liatris punctata* Hook., Asteraceae), an important nectar source.

Loess Hills specimens of *H. leonardus* showed a complete cline of characteristics from typical *H. l. pawnee* in the northern Hills, to typical (Ozark) *H. l. leonardus* in the south (Fig. 2). Populations from Monona,

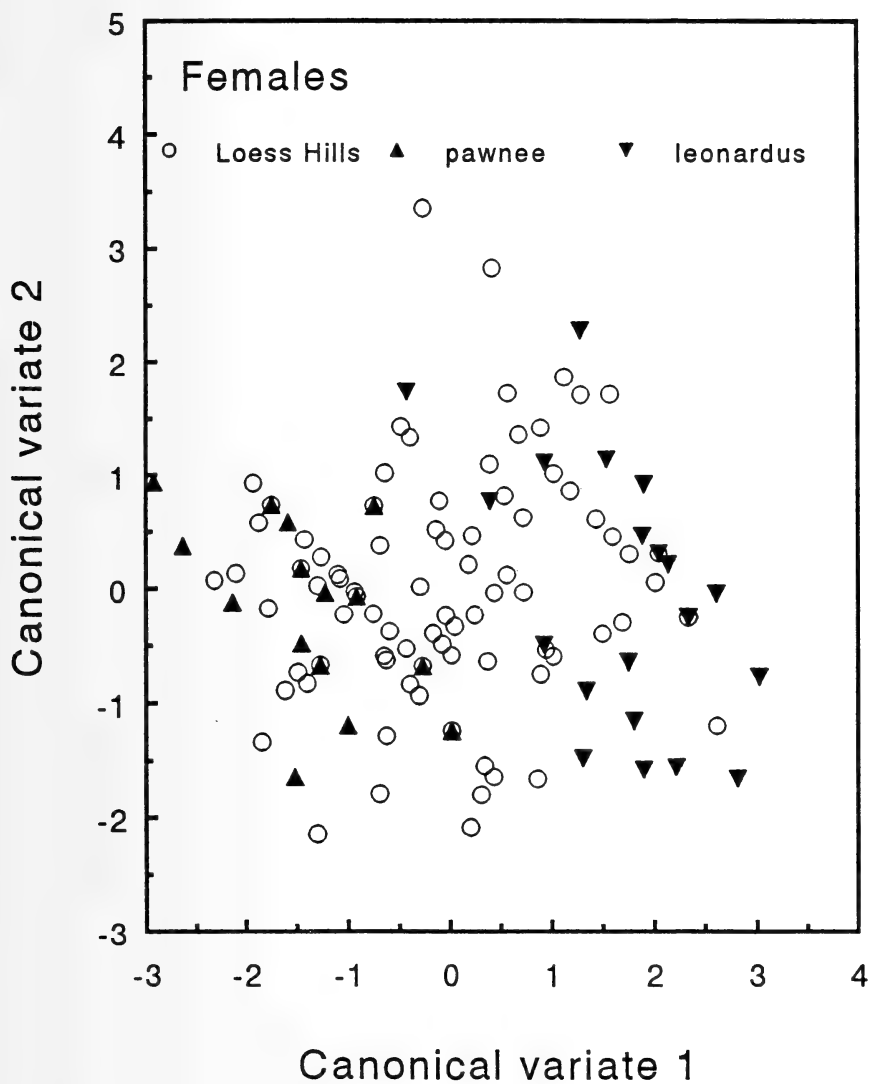


FIG. 4. Results of the canonical discriminant analysis of *Hesperia leonardus* populations—females.

Harrison, and Pottawattamie counties in Iowa showed the greatest degree of intergradation between the two taxa.

The results of the canonical discriminant analyses are shown in Figs. 3 and 4. The first canonical variate provided the most significant discrimination of specimens for both sexes ($P > 0.0001$). The second

canonical variate was not significant for either sex ($P > 0.3949$ males, $P > 0.9095$ females) but is used in Figs. 3 and 4 for ease of viewing individual points. (In other words, only the X-axis spacing of points of Figs. 3 and 4 represents significant discrimination of specimens.) Ventral hindwing median band size, fulvousness of males, ventral hindwing color, and transparency of the dorsal forewing hyaline spot in females were the most important canonical coefficients. Although both sexes of Loess Hills specimens overlapped the variation found in the reference specimens of typical *H. l. leonardus* and *H. l. pawnee*, females showed the greatest amount of variation (Fig. 3). For both sexes, Loess Hills specimens were ranked between known *H. l. leonardus* and *H. l. pawnee* specimens, although males overlapped more with *H. l. pawnee* than *H. l. leonardus*.

Results of the discriminant analyses are shown in Fig. 5. These analyses supported ranking material from Union, Plymouth, and Woodbury counties as *H. l. pawnee* and from Mills and Fremont counties as *H. l. leonardus*. Additionally, a north to south gradation from *H. l. pawnee* to *H. l. leonardus* is evident, with the greatest incidence of intermediate specimens (those with a <95% probability of being *H. l. pawnee* or *H. l. leonardus* by this analysis) in Monona, Harrison, and Pottawattamie counties.

Dendograms constructed from the cluster analyses are shown in Figs. 6 and 7. Although clusters essentially agree with the other analyses, intergrade populations from Harrison, Monona, and Pottawattamie counties are closer to *H. l. pawnee* than to *H. l. leonardus* (especially males) by this analysis. A sample of four males from Lincoln Co., Nebraska (west-central Nebraska) also clustered with the Loess Hills intergrades, apparently because of their tendency towards a darker, or less fulvous, dorsal phenotype.

All three analyses support north-to-south gradations from *H. l. pawnee* to *H. l. leonardus*, with populations in Monona, Harrison, and Pottawattamie counties representing the greatest amount of intergradation. Although some differences were noted between sexes, trends toward intergradation by location generally agreed for both males and females.

These analyses support the assertion by Scott and Stanford (1981) that *H. l. leonardus* and *H. l. pawnee* are subspecies rather than species. Other observations during this study support this conclusion. For example, a sample of male genitalia, representing typical *H. l. pawnee*, *H. l. leonardus*, and Loess Hills specimens was examined. MacNeill (1964) described differences in genitalia between *H. l. leonardus* and *H. l. pawnee*; however, Scott and Stanford (1981) stated that the genitalia of the two were too variable to detect differences. We found that

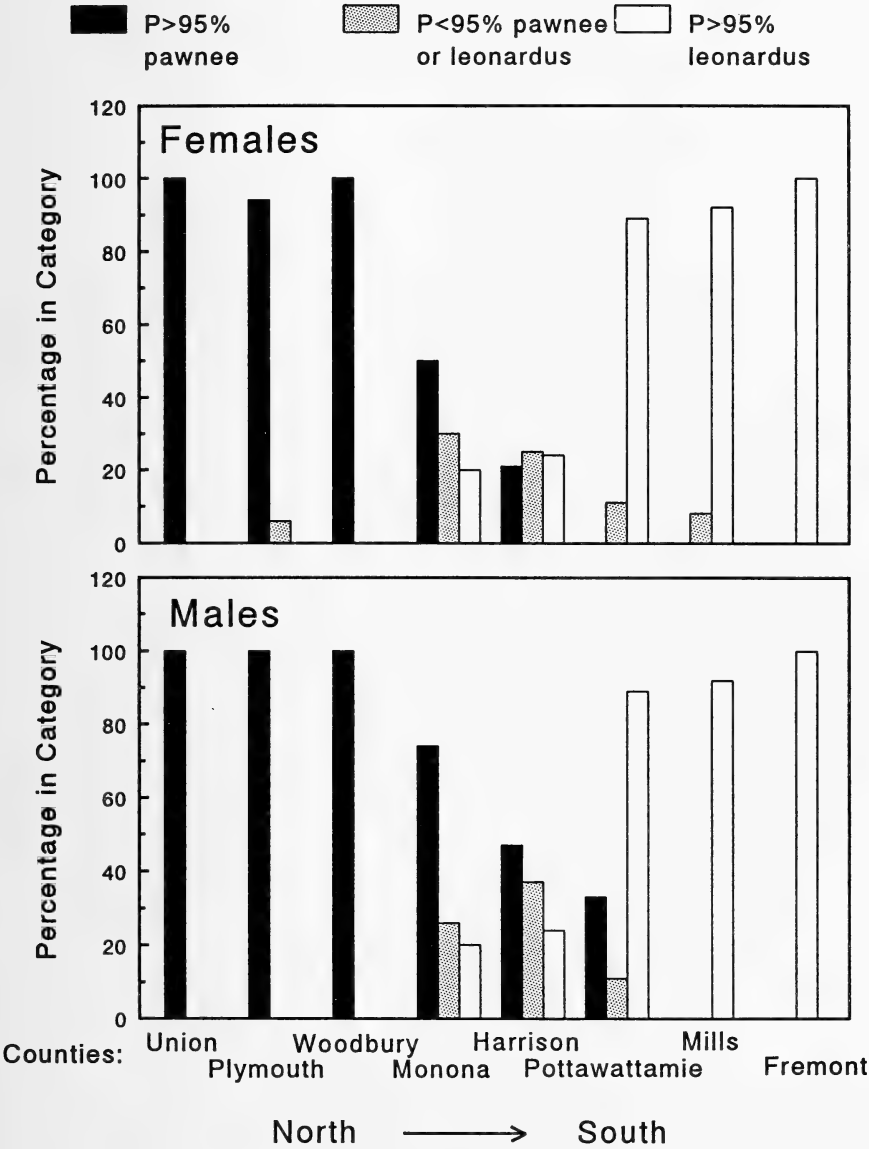
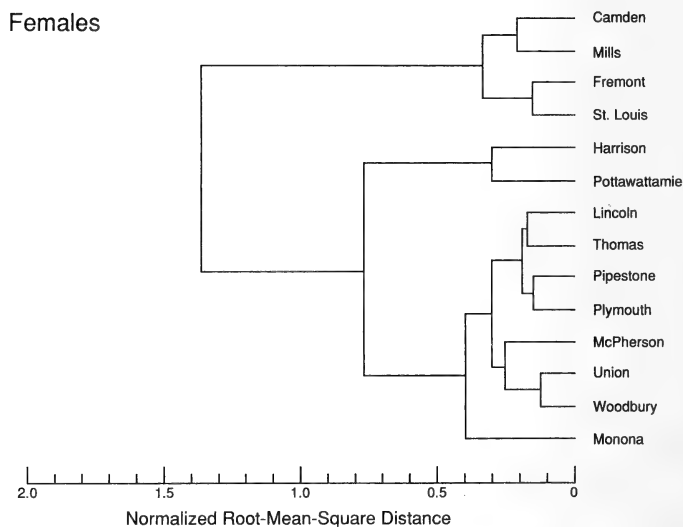
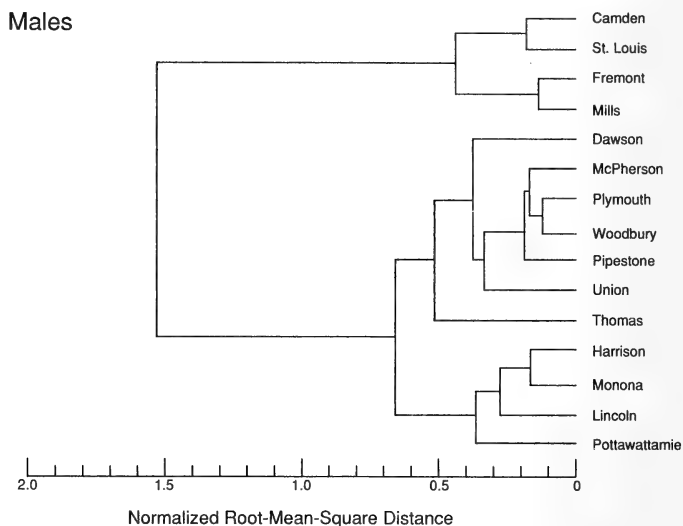


FIG. 5. Results of the discriminant analysis for male and female *Hesperia leonardus*, indicating probability of membership in a given subspecies by county (see text for details).

the degree of variability (even within one population) was too high to consider using male genitalia as a diagnostic character.

The major nectar source of the Loess Hills *H. leonardus* is blazing star, although rough gayfeather (*Liatis aspera* Michx., Asteraceae),



FIGS. 6 and 7. Dendrograms of the cluster analysis of *Hesperia leonardus* populations. **6.** Males; **7.** Females. Code for counties listed above: Camden, St. Louis = Missouri Ozarks (*leonardus*); Dawson, McPherson, Thomas, Lincoln = Nebraska (*pawnee*); Pipestone = Minnesota (*pawnee*); Union = South Dakota; Plymouth, Woodbury, Monona, Harrison, Pottawattamie, Mills, Fremont = Iowa (Loess Hills populations).

annual sunflower (*Helianthus annuus* L., Asteraceae), and thistle (*Cirsium* spp., Asteraceae) were used in the absence of *L. punctata*. All specimens from the Loess Hills showed a preference for *L. punctata* when more than one nectar source was available.

The typical habitat for Loess Hills *H. leonardus* populations was ridgetop prairie; however, specimens also were found in roadside ditches at the base of the hills in Mills and Fremont counties. Although it has been reported that *H. l. leonardus* males choose higher perches than western populations [i.e., *H. l. pawnee* and *H. l. montana* (Skinner)] (Scott and Stanford 1981), this is more than likely a function of availability of high vs. low perching sites in a particular location. We observed no differences in perching sites between *H. l. pawnee* in the northern Hills and *H. l. leonardus* in the southern Hills.

The larval host of the Loess Hills *H. leonardus* populations remains unknown. In 1989, one adult female was observed crawling around the base of little bluestem, presumably to oviposit. Recently, Wooley et al. (1991) reported that blue grama [*B. gracilis* (H.B.K.) Griffiths] was the only observed larval host for the subspecies *H. l. montana* in Colorado. Although there is little blue grama in the Loess Hills, there are sufficient stands of side-oats grama and hairy grama to provide larval resources for *H. leonardus*.

The exact factors influencing the distribution and phenotypic expression of *H. l. pawnee* and *H. l. leonardus* in the Loess Hills are unknown. However, the north-to-south transition from *H. l. pawnee* to *H. l. leonardus* appears to be a case of primary intergradation: relatively smooth character clines between contiguous populations in continuous contact (Mayr 1963). Primary intergradation is believed to be caused by corresponding changes in environmental conditions, which fits conditions associated with the variation between *H. leonardus* subspecies in this study. The scarcity of ridgetop prairies in the southern Loess Hills may be preventing the southward spread of *H. leonardus* because of fragmentation of habitat and hosts. Prairies probably were once continuous or nearly so in the Loess Hills from north to south before the elimination of prairie fires and the subsequent accelerated invasion of trees and woody shrubs. The southern Loess Hills populations of *H. l. leonardus* may have been connected to Ozark populations before disruption of habitat occurred. Increased humidity and rainfall also are associated with the increased forestation in the southern Loess Hills. The mean annual temperature also increases from north to south along the Loess Hills. Possibly humidity, or a combination of temperature and humidity, has contributed to the divergence of *H. l. pawnee* to the north and *H. l. leonardus* to the south.

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DIAPAUSE, VOLTINISM, AND FOODPLANTS OF *AUTOMERIS IO* (SATURNIIDAE) IN THE SOUTHEASTERN UNITED STATES

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ABSTRACT. *Automeris io* occurs throughout a wide latitudinal range. Across this range its voltinism is variable related to climatic conditions. It is single brooded in the northeastern United States and adjacent Canada; bivoltine in Louisiana, northern Georgia and northern Florida; trivoltine in central Florida; and multivoltine in southern Florida. With exception of southern Florida, one diapausing brood plus one or more non-diapausing broods occur annually. Freezing temperatures may increase the duration of pupal diapause 88 days or more. Florida males of the diapausing brood frequently are tawny brown in color similar to *Automeris* of the lower Florida Keys. Non-diapausing pupae cannot survive freezing temperatures. Mating behavior and mating techniques are discussed, new larval food plants observed during data collection are reported.

Additional key words: brood sequence, mating behavior, climate, phenotypic variation, rearing technique.

The Io moth, *Automeris io* (Fabricius), is one of several Saturniidae that has experienced a decline in numbers in the eastern United States in recent years. At one time considered a pest of cotton in the southern United States (Packard 1914), it has declined sharply in Florida and the Gulf States with the exception of Louisiana where it is still common. Although formerly abundant in the northeastern states, it now fluctuates from rare in mainland areas to common in Martha's Vineyard, Massachusetts, Block Island, Massachusetts (C. L. Remington pers. comm.), and parts of Cape Cod, Plymouth, Massachusetts. Dale F. Schweitzer (pers. comm.) indicates that it is common in southern New Jersey. It is never abundant in south central Pennsylvania; only 1-4 males per season were collected at UV light traps operated from dusk to dawn by Larry Kopp and myself over the past 30 years. From 1987-92 no males were taken.

From correspondence and visits with lepidopterists in Florida, it became evident that *A. io* is now apparently less common there than in the 1970's. The decline in numbers of *A. io* prompted me to expand my research from genetical analyses of the moth to factors affecting its life cycle in eastern United States. Mating behavior, diapause, and emergence patterns of *A. io* were studied.

The life history of *A. io* is well documented in published works that span two centuries, from the pioneer work of John Abbot (Abbot &

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Smith 1797) to the present (e.g., Eliot & Soule 1902, Packard 1914, Pease 1961, Collins & Weast 1961, Ferguson 1972, Weast 1989). Nevertheless, data concerning the number of broods, duration of flight periods, presence or absence of diapause, reproductive behavior, and preferred foodplants are incomplete.

This report is the result of more than ten years (1979–88) of collecting specimens, studying larvae in their natural habitat, rearing larvae for brood sequence study, and foodplant observations. All specimens collected by collaborators are deposited in the Peabody Museum of Natural History, Yale University. Specimens reared by the author in Pennsylvania are a part of the research collection at the Peabody Museum, Yale University.

MATERIALS AND METHODS

Data was collected with the assistance of fifteen lepidopterists located in areas assumed to be critical to the data base. These collaborators were selected on the basis of their familiarity with *A. io*, their ability to conduct long-term field work, and their willingness to participate in a project of several years duration. Preliminary data from these collaborators suggested that the sampling area could be divided into four regions based on the number of broods and seasonal flight period of *Automeris* (Fig. 1).

Region A comprises the Florida Keys south of Key Largo. *Automeris* collected in this area have been referred to as *Automeris io lilith* (Strecker). However, this insect is distinct from *A. io lilith* and will be described in a future publication. Region A has been sampled by Trehune Dickel, Homestead, Dade County, Florida from 1968–92.

In Region B *A. io* has four broods per year as demonstrated by sample sites at Jupiter, Palm Beach Co., Florida; Miami and Homestead, Dade Co., Florida.

In Region C *A. io* has three broods per year as demonstrated by sample sites at Kissimmee, Osceola Co., Florida and Tampa, Hillsborough Co., Florida.

In Region D *A. io* has two broods per year as demonstrated by sites at Gainseville, Alachua Co., Florida; Jacksonville, Duval Co., Florida; Decatur, Dekalb Co., Georgia; and Abita Springs, St. Tammany Parish, Louisiana. Specimens and data were obtained from the designated locality or within a twenty-five mile radius of that locality.

Whenever possible, broods in Georgia and Florida were reared under natural conditions in the vicinity of where ova or larvae were found. Larvae from genetic crosses were reared on foodplants known to be acceptable to *A. io*. Matings of adults from wild pupae collected in Georgia, Louisiana, and Florida were given a "choice test" of five host

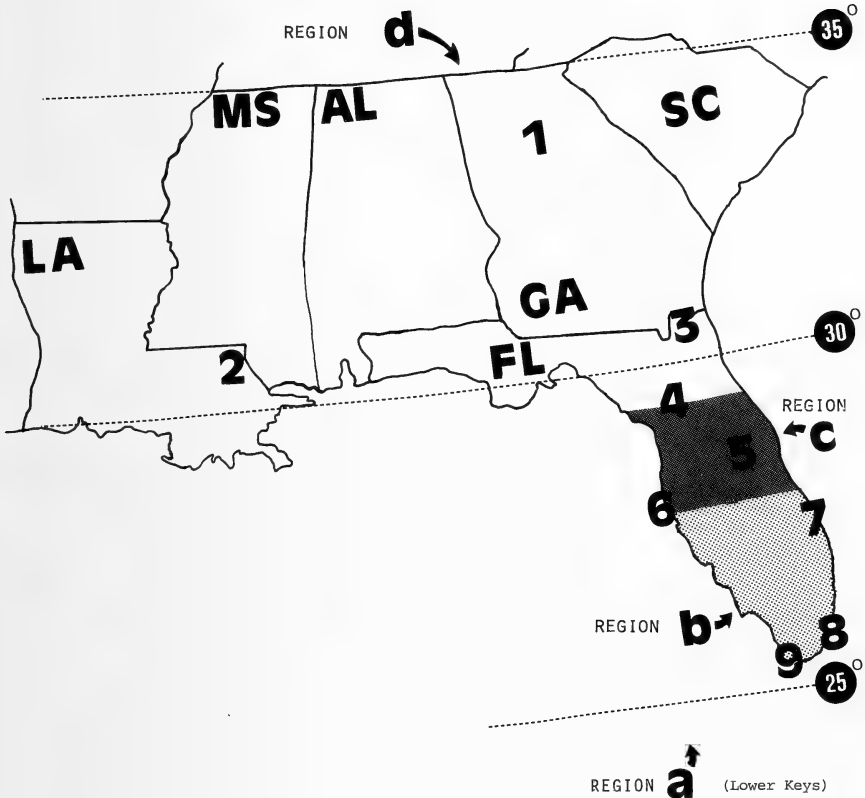


FIG. 1. Sampling Localities and Climatic Regions based on number of broods per seasons of *Automeris io*. Region A, lower Florida Keys omitted, *Automeris* in this area are not *Automeris io*; Region B, four non-diapausing broods; Region C, one diapausing brood and two non-diapausing broods; Region D, one diapausing brood and one non-diapausing brood. Numbers 1-9 areas where samples were taken. (1) Decatur, Georgia (DeKalb County). (2) Abita Springs, Louisiana (St. Tammany Parish). (3) Jacksonville, Florida (Duval County). (4) Gainesville, Florida (Alachua County). (5) Kissimmee, Florida (Osceola County). (6) Tampa, Florida (Hillsborough County). (7) Juniper, Florida (Palm Beach County). (8) Miami, Florida (Dade County). (9) Homestead, Florida (Dade County).

plant species known to be acceptable to *A. io*. Choice tests were conducted in eight inch glass containers with moistened paper towel covered bottoms. Immature and mature leaves of each foodplant offered were placed around the outer portion of the container, and the newly hatched larvae were placed in the center of the container. Larval foodplant selection usually occurred within 24 hours of hatching. When larvae were reluctant to select a foodplant the day following emergence, fresh leaves of the initial choice test plants were provided daily until the larvae selected a preferred foodplant or until they starved to death.

First instar larvae prefer fully expanded immature leaves; terminal leaf growth desiccates rapidly once removed from the branch and was rarely selected by larvae in choice tests.

Females of *A. io* mate readily if they are placed with males in a wire cage or gallon can with a wire covering; old burlap makes an excellent substrate for the copulating pair. Because copulation rarely occurs on the night of emergence of the female, males were placed in the breeding cage on the second night. Fresh leaves of an acceptable food-plant [e.g., *Prunus serotina* Ehrh. (Rosaceae)] in or on top of the breeding cage encourages females to mate and oviposit.

Fertile ova from controlled crosses were placed in petri dishes on slightly moistened paper towel material. The dishes were covered until the larvae hatched. First instar larvae were removed to small plastic containers with paper towel-covered bottoms and were fed young leaves of *P. serotina*. After the first instar molted, larvae were placed outdoors in large cloth sleeves on *P. serotina* or *P. virginiana* L. and left undisturbed for several weeks. During the final instars, sleeves were moved whenever the larvae had consumed most of the mature leaves preferred at this stage of development. Final instar larvae were placed in large screened cages with a mat of dry leaves on paper to provide a pupation substrate. Branches of the foodplant were supplied daily until all larvae spun cocoons. Leaves containing cocoons were not disturbed for 10–14 days to insure that all pupating larvae had transformed from larvae to pupae. Cocoons were removed, cleaned of excess leaves, and stored in cardboard containers at 5°C for the winter. Many cocoons of *A. io* are extremely thin and rupture when handled, exposing the pupae. Fifty percent or more of the cocoons were torn when removed from the leaves of the breeding cage; under laboratory conditions this did not affect viability. Pupae were removed from refrigeration 10–15 May each season and placed in wire cages at 21°C until eclosion (approximately 30 days). Matings in mid-June, when food supplies were ample, resulted in mature pupae in mid-September.

Collaborators ran UV light traps nightly each season (1979–85) until evening temperatures dropped below 8°C. [*Automeris io* rarely fly below this temperature.] Trapped specimens were killed, papered, and shipped to me. I spread and recorded data on all specimens as received. Wild larvae were reared in the vicinity of collaborators' homes on foodplants upon which larvae were found. In most cases larvae were not sleeved, allowing observation of predation and parasitism. Pupae and data concerning each reared brood were sent to me for analysis and recording. Foodplants supporting wild larvae were identified and checked frequently as larvae developed.

To determine the range of food plants used by *A. io lilith* in Florida,

careful observations were made while collecting ova and larvae. Food plants where larvae were observed feeding were reported by eleven collaborators over a five year period.

RESULTS

Mating Behavior

Adult *A. io* emerged from late morning to mid-afternoon. The moths remained flightless until dark. If environmental conditions were favorable (i.e., temperatures above 10°C, low wind velocity, no heavy fog or rain), males engaged in preflight posturing—a flexing and fluttering of the wings for a short period (sometimes coupled with walking on the resting substrate)—followed by several minutes of rest before flight was initiated. Unless disturbed, females remained inactive the first night following emergence. At dusk of the second night, females performed the same preflight movements as males, then remained motionless on a leaf or trunk. Around 2200 h virgin females initiated “calling” behavior, releasing an attractant pheromone by extending and retracting the last abdominal segment at two second intervals for a short period of time (1–2 minutes). The abdomen always was oriented down wind for maximum pheromone dispersal. Based on attempts to attract wild males by exposing females under a wide range of environmental conditions, it appears that strong gusty winds, heavy rain, and dense fog (conditions that inhibit dispersal of the pheromone) all inhibited calling behavior by the female. Temperatures above 10°C were critical to initiation of calling behavior; at lower temperatures the female remained motionless on the substrate. Under laboratory conditions calling behavior was observed to have a circadian rhythm; caged females “called” every evening until they were allowed to mate. Matings of *A. io* (1964–91) occurred within 5–30 minutes after the female began calling. By 2300 h tethered unmated females sometimes continued calling but wild males rarely responded beyond that time.

Based on observations of over 500 controlled crosses resulting in fertile ova, the duration of copulation is about 90 minutes. A sudden drop in temperature below 8°C usually caused the pair to remain *in copula* throughout the night or until the temperature rose to about 8°C. On warm nights wild males usually flew away soon after separation from the female. On cool nights (below 8°C) the male remained beside the female throughout the night and the following day.

Diapause

Diapause in *A. io* occurs in the pupal stage. In the northern portion of its range, obligatory diapause occurs every generation, hence, the

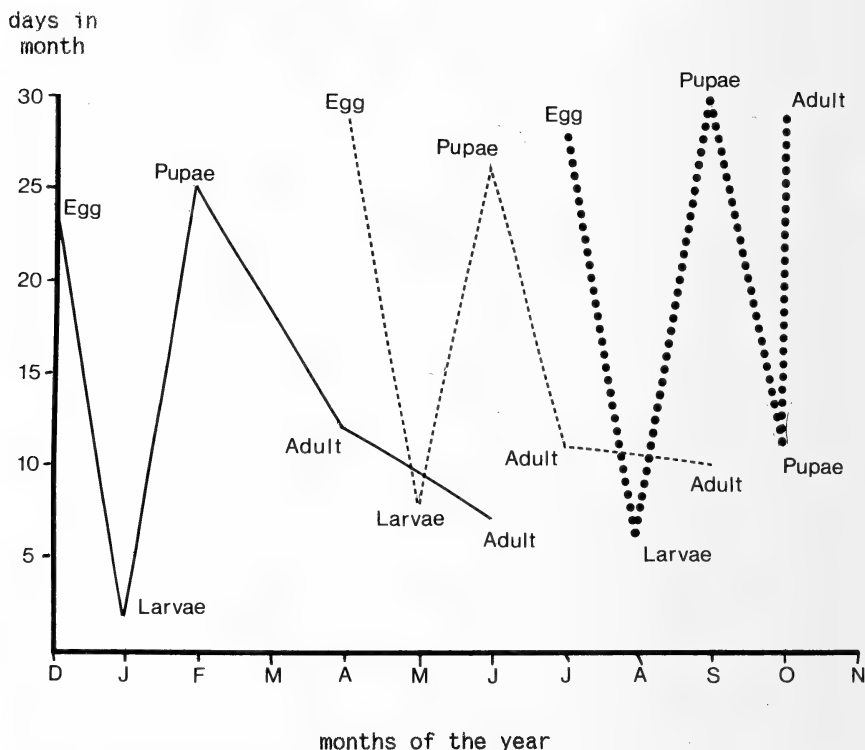


FIG. 2. Overlapping sibling brood sequences of a non-diapausing gravid *A. io lilith* female, Fort Lauderdale, Broward County, Florida, 24 December 1985 broods reared under controlled conditions. Brood 1: Eggs laid 25 December 1985, larvae 2 January 1986, pupae 26 February 1986, adults 12 April to 7 June 1986. Brood 2: Eggs laid 29 April 1986, larvae 8 May 1986, pupae 27 June 1986, adults 10 July to 9 September 1986. Brood 3: Eggs laid 29 July 1986, larvae 6 August 1986, pupae 30 September 1986–11 October 1986, adults 28 October 1986–8 November 1986. Remaining 22 pupae stored at 5°C.

species is univoltine. In the southern portion of its range, one or more non-diapausing generations are followed by a diapausing generation. In the southern tip of Florida, *A. io* was found to be continuously brooded, without diapause.

Diapause is controlled by photoperiod in many insects (Beck 1962, 1963, DeWilde 1962). Photoperiodism in facultative diapause affects every generation, however, the generation developing during late summer under decreasing day length enters diapause to survive the winter (Lees 1955, DeWilde 1962, Bursell 1964). The short day photoperiod, 12 hours or more of darkness per 24-hour day, applies to *A. io* as all diapausing generations occurred late in the season with pupation from September to November. Controlled crosses of *A. io* in early 1970's, of

matings made in May with pupation in late August or early September, had a small percentage (8 to 15%) of non-diapausing males emerge in early October. Pupae from May matings that were refrigerated at 5°C as soon as they pupated had 10–15% greater pupal decomposition or desiccation during winter storage than the normal 3–5% that occurs in pupae from June matings. This suggests that those mortalities represent non-diapausing pupae. Offspring from matings ($n = 400+$) made in mid-June with pupation occurring in late September all appeared to diapause with minimal mortality during winter storage.

Males of diapausing generation of *A. io lilith* in Florida are phenotypically distinct from those of the non-diapausing generation(s). Males from diapausing pupae are tawny brown, whereas males from non-diapausing pupae are yellowish with a light suffusion of rosy-red scales. Dominick reported a similar situation in the bivoltine *A. io* in eastern South Carolina (Ferguson 1972:161).

Once diapause is induced, the duration of dormancy is influenced by temperature and moisture. In Pennsylvania and mountain regions north of Region D (Fig. 1), the thickness, amount of leaves and debris spun in fibers of the cocoon, the insulation effects of leaf cover, and depth and duration of snow and frost are factors that control developmental responses in diapausing pupae (Manley et al. unpubl. data). In Pennsylvania, warm weather during March and April usually results in the early emergence of many species of moths, including *A. io* (unpubl. data).

Non-diapause

Samples of *A. io lilith* pupae collected or reared during the winter months (Nov.–Feb.) in southern Florida and Key Largo (Region B, Fig. 2A) did not diapause. Non-diapausing pupae are sensitive to temperatures below 5°C and experience high mortality (90%) below this threshold. During 1984 four different broods of reared or wild pupae from Region B (Fig. 1) were shipped to Pennsylvania. Of nineteen pupae shipped from Jupiter, Florida to Pennsylvania during below freezing temperatures (5 January 1984), none hatched. Sibling pupae ($n = 34$) from the same brood reared in Florida were shipped 20 April 1984. Three males hatched during shipment, and the remaining 25 males and 6 females hatched in late April and May. Small samples of non-diapausing pupae from southern Florida shipped during warm periods when temperatures were above freezing, survived and began emerging shortly after arrival when held at 22°C.

The sequence of non-diapausing overlapping broods is shown in Fig. 2. These data represent the progeny of a wild female taken at UV light on 24 December 1985 at Fort Lauderdale, Broward County. Larvae

A. REGION B

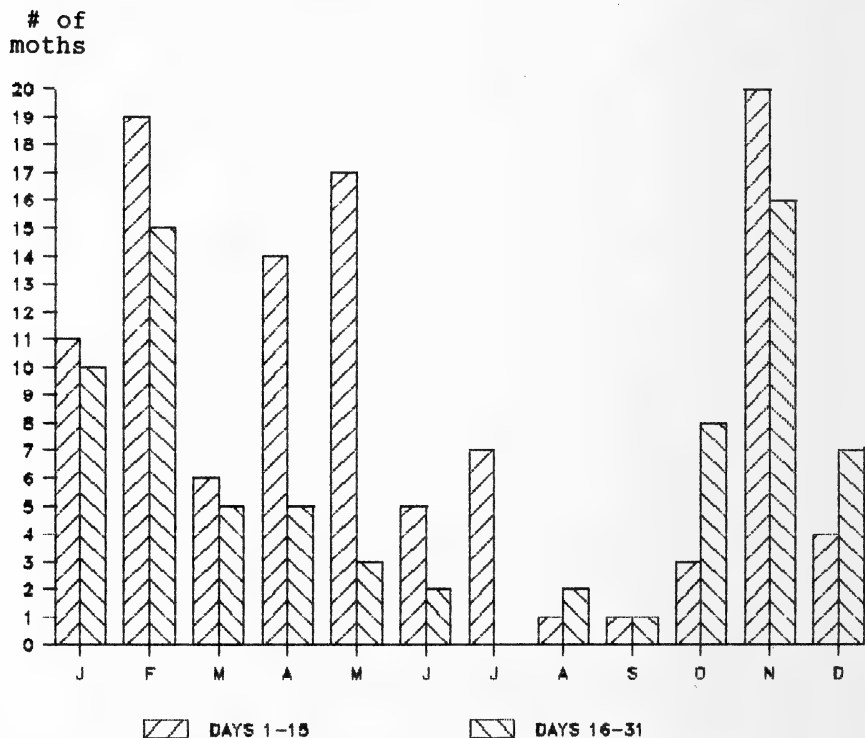


FIG. 3A. The flight periods and brood sequences of *Automeris io lilith* determined from males taken at UV light traps. Each bar represents a 15 day sample over a five or more year period. The diapause brood is black, non-diapause brood white. A) Region B, southern Florida ($n = 103$) 1983-87 show four non-diapausing broods annually; B) Region C, central Florida ($n = 303$) 1980-88 show one diapausing brood February-April, two non-diapausing broods May-July and August to November; C) Region D, northern Florida ($n = 166$) 1983-87 show an extended diapausing brood late March to June and one non-diapausing brood July-November. June population maybe mixed with late emerges of the diapausing brood and early emerges of the non-diapausing brood. Non-diapausing individuals of the diapausing brood could be flying in October-November.

were reared in Florida on *Ficus benjamina* L. (Moraceae) and pupae were taken to Decatur, DeKalb County, Georgia by Hermann Flaschka. Sibling matings were conducted on 29 April 1986, and larvae were reared on *Prunus serotina* L., with pupation about 26 June 1986. These pupae were sent to Pennsylvania, where third brood sibling matings were made 29 July 1986. Larvae were offered a choice of the following woody plants: *Prunus serotina* L., *Syringa vulgaris* L. (Oleaceae), *Hibiscus palustris* L. var. *disco belle* (Malvaceae), *Ficus benjamina* L., and *Quercus acutissima* Carruthers (Fagaceae). First instar larvae chose

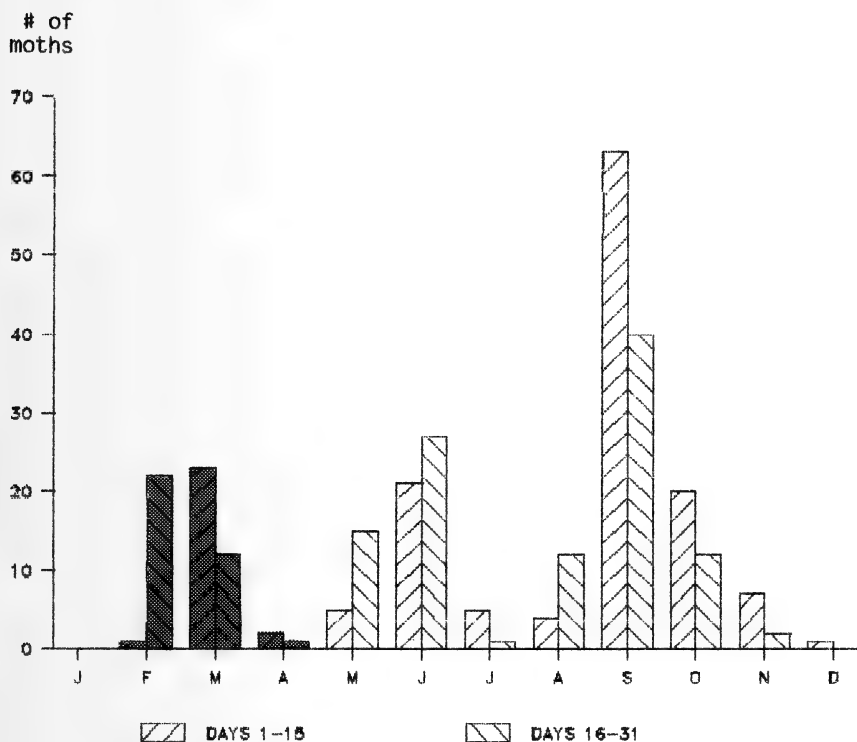
B. REGION C

FIG. 3B. See caption for Fig. 3A.

Q. acutissima and were sleeved outdoors on this plant until they pupated in late September. Three males emerged 28 October and 6 and 8 November 1986. The remaining pupae ($n = 22$) of this non-diapausing population were stored at 5°C to determine if they could survive the winter; by early February all stored pupae and died.

Figure 2 demonstrates the overlapping brood sequence of *A. io lilith* in southern Florida. Circumstances prohibited the rearing of the fourth brood as no cooperator in southern Florida was available to rear it. Sibling matings of brood 3, normally flying in September and October in Florida, would have resulted in adults in December to complete the yearly cycle. Specimens have been collected every month of the year in Region B (Fig. 3A).

Diapause Duration

The survival of pupae shipped from Florida to Pennsylvania during below freezing temperatures suggests that diapausing pupae of *A. io*

C. REGION D

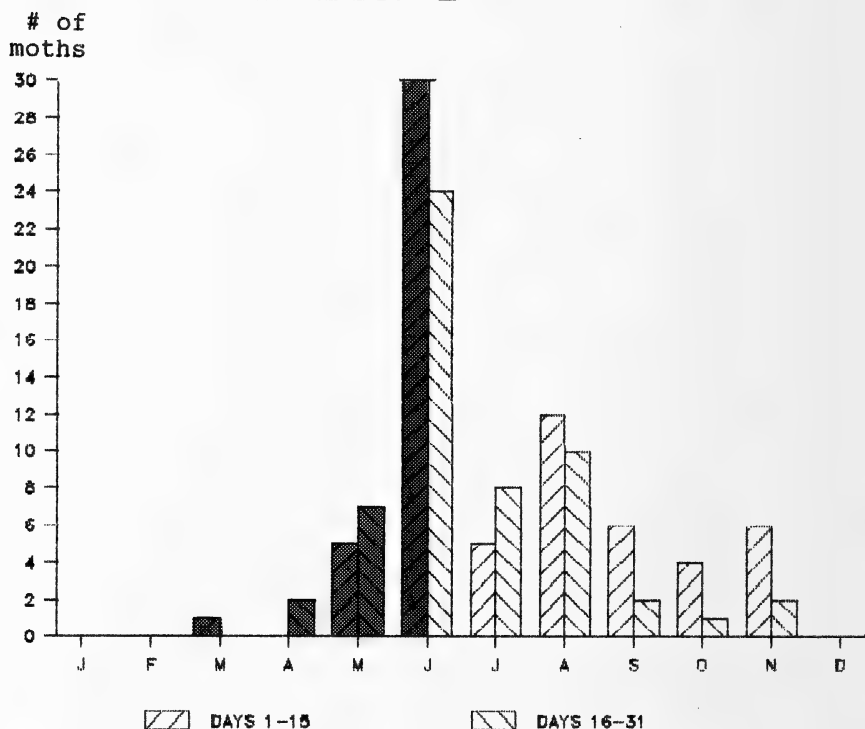


FIG. 3C. See caption for Fig. 3A.

lilith from central and northern Florida respond to sub-freezing temperatures by prolonged diapause. Cold hardiness of pupae of northern *A. io io* is demonstrated by the tolerance to a wider range of fluctuating and cold temperatures, often below -18°C . Over a three year period pupae ($n = 25+$) were placed in cloth or net mesh bags laid on the ground exposing them to outdoor conditions in Pennsylvania from November to June when they began to emerge as adults. Their emergence was predictable in that it coincided with the normal flight period of wild *A. io io* mid-June to mid-July.

Frequent Florida shipments of wild pupae collected by cooperators from Gainesville, Alachua County, southward to Tampa, Hillsborough County, during December and January 1985-86 were subjected to five or more days of below freezing temperatures en route to Pennsylvania. Pupae subjected to night temperatures -10°C to -15°C , day temperatures -4°C to -8°C , at some period during shipment north (30 to 40%) showed an extension of diapause emerging 88 to 121 days later than expected. Males from diapausing pupae normally emerging in

mid-February to mid-April, emerged in August. These males were deep tawny brown typical of males from diapausing pupae in Florida. Sibling matings produced fertile ova in mid-August.

Diapausing pupae are able to survive exposure to below freezing temperatures during shipments north whereas non-diapausing pupae from southern Florida during the winter of 1985–86 were not able to survive. Larvae developing into pupae shipped in 1985–86 from the Tampa area fed during the short days of the late fall months when daily temperatures were 27–32°C.

Short periods of below freezing temperatures are common in the northern portion of Region C (Fig. 1), thus it is anticipated that periods of below freezing temperatures frequently would extend emergence of the diapause brood three weeks or more, depending on the duration and frequency of freezing temperatures. Late emerging adults of the diapause brood would be flying concurrent with the non-diapause summer brood. Tawny brown males of the diapause brood may appear in midsummer when yellow non-diapause males are flying. The appearance of brown males in the cooperators' five year samples varies in Regions C and D as does the number of below freezing periods in each during a particular season.

Emergence Patterns

Univoltine populations. *Automeris io* populations in its northern range are univoltine (Collins & Weast 1961, Ferguson 1972). Emergence varies from late May to mid-July in Pennsylvania, with a similar emergence pattern in New England and southern Canada. Wild males taken at UV light traps near Liverpool, Snyder County and Klingerstown, Schuylkill County, Pennsylvania show flight from 5 June to 17 July (one male taken on 5 August 1965); the majority of specimens were taken between June 14 and July 12. The flight period in Connecticut, deduced from the UV light samples of Sidney A. Hessel and the extensive collections (1950–60) of Charles L. Remington in the Peabody Museum, ranges from 2 June to 18 July (one early emergence of 12 May 1958). In southern New Jersey the extensive collections (1980–86) of Dale F. Schweitzer range from 10 June to 10 July with an occasional early or late emergence. These data suggest a six week flight period for univoltine populations.

Ferguson (1972:159) cited observations by M. C. Nielsen in Michigan of a small second brood; these are surprising, as our intensive studies in Pennsylvania showed no wild males coming to light in August and September. In captivity it is common for this and other univoltine Lepidoptera to show a partial hatch late in the year. Presumably, these late partial broods lack diapause and produce no surviving descendants.

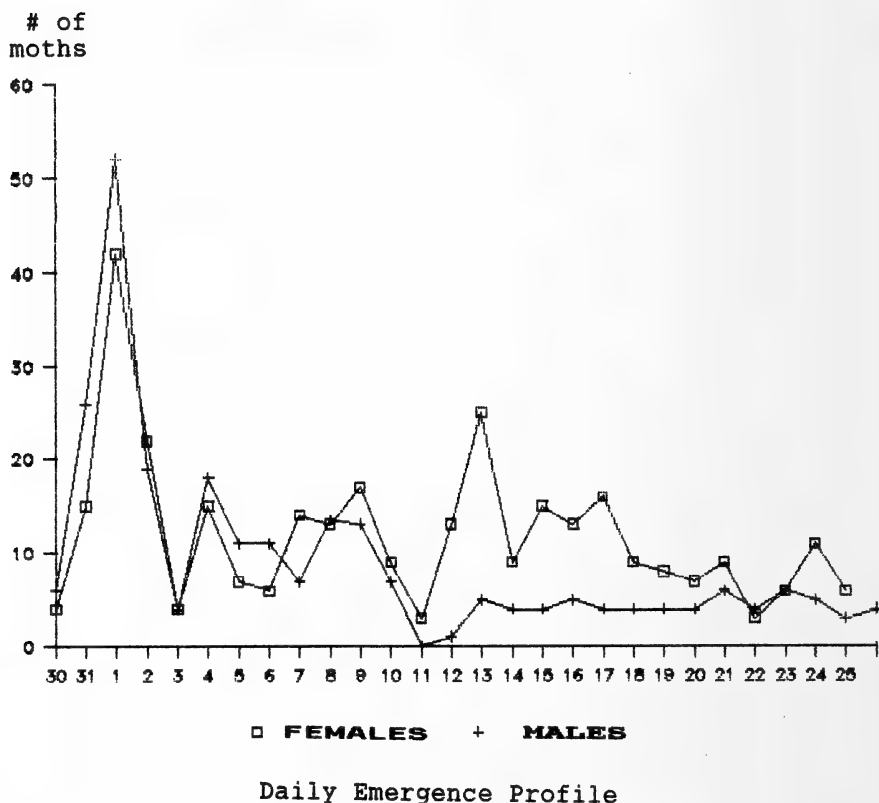


FIG. 4. Daily Emergence Profile of males and females from five crosses of Pennsylvania *Automeris io io* ($n = 234$ males, 140 females). Initial emergence 30 May 1985, final emergence 25 June 1985.

A series of crosses was made to determine the emergence pattern of females in relation to males in captivity and to evaluate sexual differences in emergence. Emergence data were taken from five univoltine crosses made in 1985 (Fig. 4). The range of emergence of these univoltine crosses was from 30 May to 28 June with no differences between sexes.

Bivoltine populations. Populations of *A. io* in coastal South Carolina, eastern Gulf Coast states (Georgia to Louisiana) and northern Florida (Fig. 1, Region D) appear to be bivoltine (see Fig. 5 and Fig. 3C). Sampling in the Murphy-Buford area of northern Georgia by Hermann Flaschka during 1979–85 (Fig. 5A) showed an extended diapausing brood, with the emergence of non-diapausing males in September (and possibly in October, as Dr. Flaschka usually terminated his UV light sampling in mid-September).

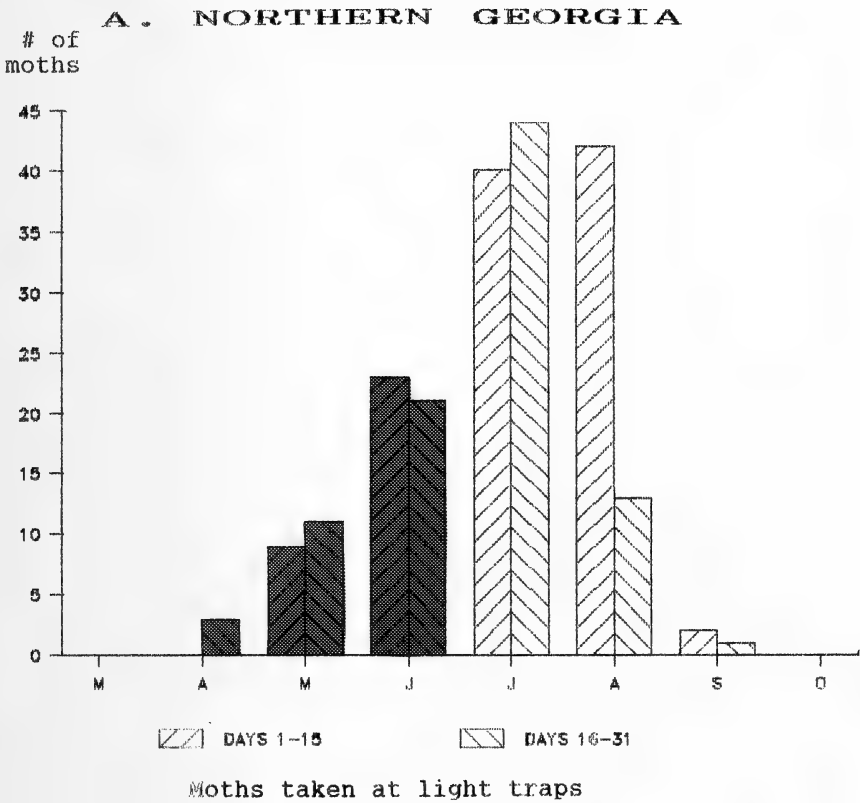
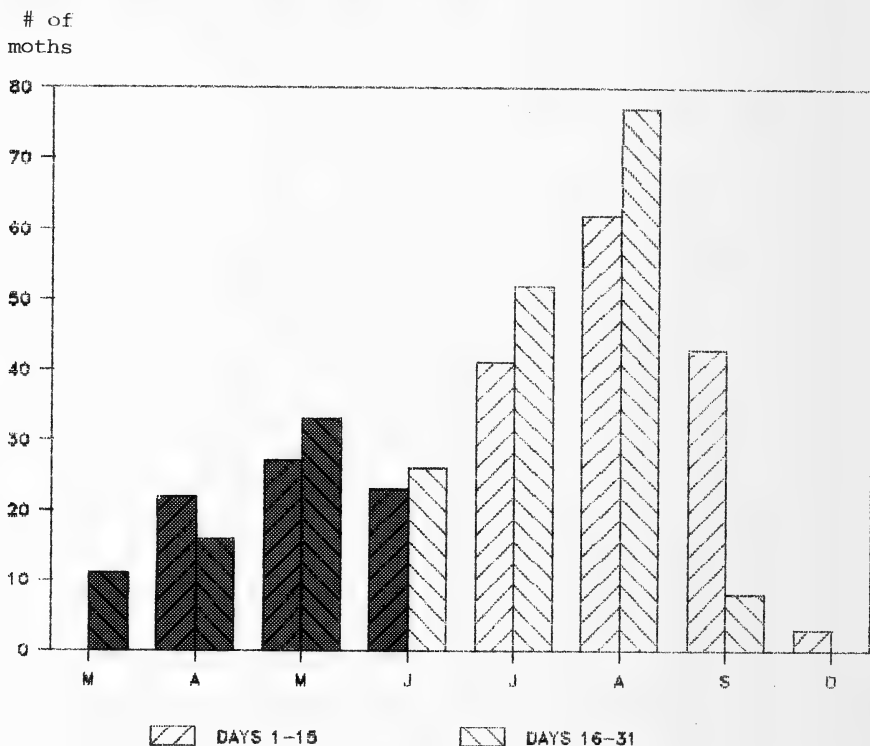


FIG. 5A. The number of male *Automeris io io* moths taken at UV light traps. Each bar represents a 15 day sample over a period of five or more years of a bivoltine population. The diapausing population is black, the non-diapausing population is white. A prolonged emerging diapause brood March to June gives rise to a large non-diapausing brood in July to September. The June population may be a mix of late emerges from the diapause brood and early emerges of the non-diapausing brood. A) Northern Georgia (n = 207) 1979-83; B) Southern Louisiana (n = 833) 1979-85.

In the 1969-70 crosses of Pennsylvania *A. io*, I observed that May matings produced a small percentage of non-diapausing pupae: 1969, 6 males and 5 females (n = 152 pupae) in late August and September; 1970, 27 males and 2 females (n = 255 pupae) in September and early October. In order to control fall emergence of May matings, mature pupae were refrigerated in early September at 5°C. This procedure produced 10-15% more mummified and decomposed pupae than occur in June matings. I concluded that many of these additional dead pupae were non-diapausing individuals that died during the long period of refrigeration. Future breeding programs (1971-86) were based on mid-

B SOUTHERN LOUISIANA

Moths taken at light traps

FIG. 5B. See caption for Fig. 5A.

June to early July matings, which matured in September, and all appeared to diapause.

Samples by Vernon Brou in St. Tammany and St. John's Parish in southern Louisiana (1979-85) illustrate a bivoltine life cycle with the emergence of many non-diapausing males in September and October. This sample area is 410 km further south than the Georgia sampling area. Matings from an extended diapausing brood flying late March to June produce non-diapausing adults flying from July to mid-September which in turn produce a diapausing brood; non-diapausing males of the diapausing brood emerge in September and October. One could expect non-diapausing *A. io* males from the diapausing brood to fly any month in the late fall and winter season in southern Louisiana. Our sample of 833 adults shown in Fig. 5B gave a 213 day flight period.

TABLE 1. Families of Florida food plants supporting larvae of *Automeris io lilith*, the name of the observer, year of observation and number of observations of each species are shown. Florida food plants previously listed Kimball (1965) are included.

Family Species	Source	Number of observations
Gramineae		
<i>Zea mays</i> L.	Kimball 1965	1
Myricaceae		
<i>Myrica cerifera</i> L.	Slotten 1985 Baggett 1984	2
Moraceae		
<i>Ficus benjamina</i> L.	Flaschka 1985	1
<i>Celtis laevigata</i> Willd.	Ritland 1985 Kimball 1965	2
Fagaceae		
<i>Quercus acutissima</i> Carr.	Manley 1985	1
<i>Quercus virginiana</i> Mill.	Baggett 1984	2
<i>Quercus laurifolia</i> Michx.	Baggett 1984	1
<i>Quercus laevis</i> Willd.	Baggett 1984	1
Lauraceae		
<i>Persea americana</i> Mill.	Kimball 1965	
Leguminosae		
<i>Cercis canadensis</i> L.	Baggett 1984	1
<i>Phaseolus vulgaris</i> L.	Kimball 1965	
<i>Galactia glabella</i> Michx.	Kimball 1965	
<i>Galactia elliottii</i> Nutt.	Kimball 1965	
<i>Amorpha fruticosa</i> L.	Kimball 1965	
<i>Wisteria sinensis</i> Sims	Baggett 1989	1
Rosaceae		
<i>Prunus serotina</i> Ehrh	Minno 1987 Flaschka 1985	3
<i>Rosa rugosa</i> Thunb.	Kimball 1965	
Magnoliaceae		
<i>Magnolia virginiana</i> L.	Baggett 1984	1
Malvaceae		
<i>Hibiscus tiliaceus</i> L.	Kimball 1965	
<i>Hibiscus palustris</i> L.	Jamieson 1984 Jolly 1984 Minno 1987 Dickel 1987, 1986 Kutash 1985 Baggett 1984, 1985 Slotten 1985	9
<i>Gossypium herbaceum</i> L.	Kimball 1965	
Cornaceae		
<i>Cornus florida</i> L.	Baggett 1984	1
Ericaceae		
<i>Rhododendron catawbiense</i> Michx.	Baggett 1987, 1984	2
<i>Rhododendron japonicum</i> Gray	Kimball 1965	
<i>Rhododendron kaempferi</i> Planch.	Kimball 1965	

TABLE 1. Continued.

Family Species	Source	Number of observations
Hamamelidaceae		
<i>Liquidambar styraciflua</i> L.	Baggett 1984 Lemberger 1984	3
Salicaceae		
<i>Salix caroliniana</i> Michx.	Kutash 1984 Ritland 1986 Lemberger 1984 Baggett 1986 Minno 1987	5
Turneraceae		
<i>Turnera ulmifolia</i> L.	Kimball 1965	
Bignoniaceae		
<i>Tabebuia argentea</i> Britton	Kimball 1965	
Ulmaceae		
<i>Trema micrantha</i> Blume	Dickel 1985 Baggett 1984	2
Palmaceae		
<i>Rhapis flabelliformis</i> L'Her.	Kimball 1965	
<i>Sabal palmetto</i> Lodd.	Kimball 1965	

The non-diapausing brood produced the greatest number of adults (Fig. 5B).

Northern Florida (Fig. 3C) was not as extensively sampled as other areas, however, continuous seasonal UV light sampling of other species of moths by H. D. Baggett, M. C. Minno, D. B. Ritland, and J. R. Slotten in the Gainesville-Jacksonville area recorded the appearance of *A. io* coming to their light traps 1983 to 1989. From these observations plus specimens of *A. io* in their collections, sufficient data were accumulated to estimate the flight periods of *A. io* in the southeastern portion of Region D (Fig. 3C).

Populations in northern Florida may encounter climatic conditions not normally encountered in central Florida. Unpredictable and severe frosts and freezes from December through March may kill larvae from matings of non-diapausing individuals. This portion of Florida is subject to jet stream patterns that bring cold air from the north; it is the coldest portion of the state, generally 4–7°C cooler than Region C to the south. The region also has the greatest diurnal temperature variation in March and April: 4–10°C at night to a high of 21–27°C in daytime. Frequent low temperatures during winter months impact the diapausing brood by delaying spring emergence and temperature of 0°C or lower may cause a "shock effect" on diapausing pupae, lengthening the emergence period into mid-summer.

Multi-voltine populations. Central Florida, a region north of Tampa, Hillsborough County and south of Orlando, Orange County, encompasses the southernmost extension of the Lower Austral life zone and the northern extreme of the sub-tropical life zone. The botanical "Fall Line", the northernmost extension of subtropical plants susceptible to cold temperatures, is in this area. Kissimmee, Osceola County, lies on this line and is in the center of Region C. Winter temperatures are moderate in this area, with cool nights (5°C) and occasional frosts in the northern portion. December and January are generally cool, but extreme fluctuations rarely occur. Frank Hedges collected UV light samples February to December 1980–82, 1986–88 shows a three brood sequence (Fig. 3B).

The diapausing brood adults emerge from late February to early April; matings of this brood produce Brood 2 (a non-diapausing brood) in late May to early July; matings from Brood 2 produce Brood 3 (a non-diapausing brood) in late August to October; matings of Brood 3 produce the diapausing brood in late September and October. Non-diapausing individuals of the typically diapausing brood fly in November.

Southern Florida (Region B, Fig. 3A) lies south of a line defined by Bradenton-Sebring-Port Pierce extending southward to Key Largo. Region A, Florida Keys south of Key Largo, is so designated as *Automeris* flying there are not *A. io lilith*. This subtropical area has abundant rainfall and warm night temperatures. Four or five non-diapausing broods fly in southern Florida. Cooperators report frequent observations of parasitized larvae. Larvae and one ova sample collected in this area were found to be heavily parasitized by braconid wasps suggesting cyclic reduction in adults during various seasons of the year. Another serious factor affecting abundance of *Automeris* in southern Florida is wild habitat destruction especially in the Keys.

Larval Foodplants

Tietz (1972:363–365) lists sixty foodplants for *A. io*, including most major groups of angiosperms. Tietz (1972) records a single conifer, *Abies balsamea* L. (Pinaceae), but this may not be a valid record. Over the last 25 years of breeding experiments with *A. io*, Larry Kopp and I have provided newly hatched larvae food choice tests covering a wide range of native trees and shrubs listed by Tietz (1972). This always was done when a new source *A. io* breeding stock was received from areas other than Pennsylvania. Native wild cherries, *Prunous serotina*, *Prunus pensylvanica*, and *Prunus virginiana*, were included in each taste test and were consistently preferred of all other food plants by first instar larvae of *A. io* originating north of central Georgia and southern

Louisiana. Larvae of all research crosses of *A. io* have been reared on wild cherry (*P. serotina*). Currently (1989-91) I am breeding *A. io* from Colorado where cooperators are compiling a list of new food plants as they collect larvae for this study. I have experienced no difficulty rearing Colorado larvae received in varying stages of instar development on wild cherry despite the fact that earlier instars fed on native Colorado plants and shrubs not indigenous to Pennsylvania.

Table 1 lists the 32 reported food plants (17 families) of *A. io lilith* in Florida. Food plants listed by Kimball (1965) are included.

Hibiscus, widely planted in urban areas, appears to be the most common food plant for *A. io lilith* in Florida. In native areas, *A. io* larvae were found most frequently on *A. caroliniana*. Florida larvae reared in Pennsylvania preferred black willow (*Salix nigra* Marsh) (Salicaceae) over pussy willow (*Salix discolor*) Muhlenb., white willow *Salix alba* L., weeping willow *Salix babylonica* L., and *P. serotina* offered in choice tests. Due to scarcity of *S. nigra*, final instar larvae were fed *P. serotina*, but with limited success as voracious feeding typical of this instar ceased. One of the most successful southern Florida broods was reared in Pennsylvania on *Quercus acutissima* Carr (Fagaceae).

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GENERAL NOTES

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ADDITIONAL NORTH AMERICAN RECORDS OF *EUCOSMOMORPHA ALBERSANA* (TORTRICIDAE: ENARMONIINI)

Additional key words: Michigan, Kentucky, Palaearctic.

The first North American record of the widespread Palaearctic olethreutine *Eucosmomorpha albersana* (Hübner) was of a single male from Midland County, Michigan, collected in 1961 (Miller 1983). Dang and Parker (1990) mentioned Saskatchewan, Canada as a locality for this species but did not include details of the collection other than that the Canadian National Collection is the depository. The purpose of this article is to report collections of a second Michigan specimen and two northern Kentucky specimens. These moths were attracted to a combination of lights, including two 20 watt blacklight tubes and a single 275 watt sunlamp. All three specimens are currently in the author's private collection.

One male (forewing length 5.5 mm) was captured on 13 June 1988, in Otsego County, Michigan. After a token effort to identify the specimen was unsuccessful, it was put away with other undetermined material. On 9 July 1991, a similar but smaller male (forewing length 4.2 mm) was captured in Big Bone Lick State Park, Boone County, Kentucky. These two individuals were obviously conspecific. A subsequent check of their genitalia confirmed that both were *E. albersana*.

A female (forewing length 4.5 mm) was captured in the same Kentucky locality on 4 August 1989. This specimen initially was misidentified as *Dichrorampha leopardana* (Busck), another olethreutine similar in size and color to *E. albersana* and with which it may be confused. All three of the specimens reported here have the intricate forewing pattern noted by Miller (1983).

Moth populations in Big Bone Lick State Park have been well sampled by the author and others. No regular schedule has been followed, but visits to the park to collect moths have occurred approximately monthly during spring and summer for the past 15 years. These activities have produced specimens of *E. albersana* only recently. It appears this species is a newcomer to the local fauna.

In the Palaearctic, larvae of *E. albersana* are leaf rollers on *Lonicera* and *Symphoricarpos*, genera of Caprifoliaceae (Miller 1983, Kuznetsov 1978). Plants in these genera occurring in Big Bone Lick State Park include *L. japonica* Thunb., *L. maackii* Maxim., and *S. orbiculatus* Moench. Although a North American host has not yet been reported, it seems likely that at least one of these plant species is a host locally.

The Palaearctic distribution of *E. albersana* extends from United Kingdom and Scandinavia south to the Mediterranean Sea and east across Europe and Asia as far as the Amur Region of Russia (Miller 1983, Kuznetsov 1978).

The relatively recent discovery and spotty distribution of *E. albersana* on this continent suggest that it is a species only recently introduced, probably on more than one occasion. Collections from three of the past five years suggest a sustained population. There can be little doubt that *E. albersana* is an extant part of the North American fauna.

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NOTES ON THE NATURAL HISTORY OF *ACHLYODES SELVA* (HESPERIIDAE) IN COSTA RICA

Additional key words: life cycle, seasonal abundance, larval behavior.

Skippers of the widely distributed Neotropical genus *Achlyodes* Hubner 1819 exploit various Rutaceae, including cultivated *Citrus* Linnaeus 1735, as caterpillar food plants (Moss 1949, Kendall 1965, Kendall & McGuire 1975, Biezanko et al. 1974, Beutelspacher 1980). In spite of its broad distribution in Central America, Mexico, and South America (Evans 1953), *A. selva* Evans is poorly studied. In this note I report certain aspects of the natural history of *A. selva* in Costa Rica.

Between September 1985 and March 1991, *A. selva* was studied at a *Citrus* bush (approx. 2.0 m tall) located on the campus of the University of Costa Rica in San Pedro Montes de Oca (9°57'N, 84°01'W), San José, San José Province. An initial examination of this bush revealed the presence of several hesperiid larvae concealed in tent shelters, prompting me to rear the caterpillars to the imago and identify the skipper. Subsequent examinations of this bush were conducted to record the abundance of caterpillars, pupae, pupal shells, and tent shelters. The abundance of flush leaves on the bush, easily distinguished from older, dark green leaves by their yellow-green color, also was recorded. At various times small numbers of caterpillars were collected and reared in clear-plastic bags containing cuttings of citrus. Caterpillar behavior in the wild and captivity was noted, especially with regard to shelter construction.

Early stages. Egg not observed. Larva in all instars with strongly dorso-ventrally flattened body profile. Head capsule strongly lobed (heart-shaped) and reddish-brown in all instars, with paired black spots laterally at base. Legs yellowish. Ground color of body bluish-green, with a lemon-yellow collar or integumental fold between body and head capsule. All instars (Fig. 1) with a bright yellow dorso-lateral line running along each side of the entire body length, consisting of closely spaced irregular shaped slashes. Anal clasper and plate with a lateral yellow ridge. The third to the last body segment bears dorsally a median cluster of small yellow dots. No pronounced changes in the color of the larva between earlier and later instars. Very similar to the description of the larva *A. thraso* Hubner, but considerably different from that of *A. busirus* (Cramer) (Moss 1949). From an initial body length of 3-4 mm, the mature larva attains a body length of 45-48 mm in about 25 days. The reddish-brown stout pupa is about 21 mm long and covered with a bluish-white flocculence or bloom (see also Moss 1949), and lasts about two weeks. There is little sexual dimorphism in adult wing size and color (Fig. 1).

Larval behavior. Larvae in all instars construct individual tent shelters in which they perch while not feeding. Larval feeding was not observed in the wild. In late instar larvae, this shelter is often made by anchoring two adjacent large leaves together with silk (Fig. 1). The larva perches on a thin silken webbing on the dorsal surface of the lower leaf and over which is tied a second leaf in a partially overlapped manner (Fig. 1). Shelters

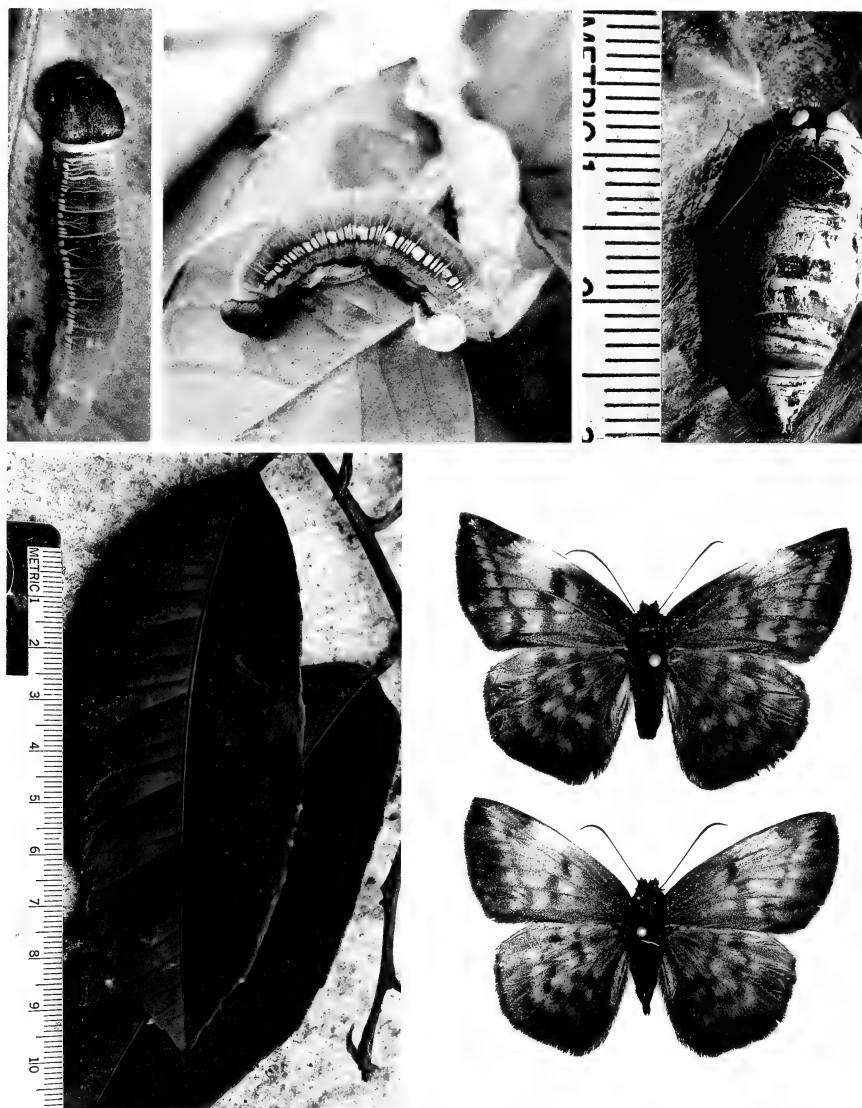


FIG. 1. Some aspects of life cycle and larval behavior in the Neotropical skipper *Achlyodes selva* Evans in Costa Rica. Clockwise, from upper left: early instars of the larva; pupal shell inside opened tent shelter, and showing whitish bloom; shelter made by a large larva pulling together and anchoring with silk two large leaves of *Citrus*; adult female (above), male (below).

of this size and arrangement often contain pupae and empty pupal shells (Fig. 1). Empty pupal shells equate to successful eclosions. No mummified or otherwise dead pupae were found, even though parasitism occurs (see below). All pupa cases were found inside shelters made with mature leaves. Small larvae make the shelter by partially excising a piece of

TABLE 1. Censuses of caterpillars, pupae, pupal shells, and larval shelters of *Achlyodes selva* Evans 1953 on a lone *Citrus* shrub, San José, Costa Rica, in relation to different time of the year and affiliated leaf flushings.

Census date	% of flush leaves	Nos. of caterpillars						No. of pupae	No. of pupal shells	No. of empty larval shelters	
		Instar	1	2	3	4	5				Total
20-IX-85	25%		8	6	5	3	3	26	2	6	10
19-II-86	0%		0	0	0	0	0	0	0	2	3
5-VIII-86	30%		3	5	2	6	6	22	0	1	8
9-XI-86	15%		0	0	4	3	2	9	0	4	5
11-III-87	20%		2	2	0	0	0	4	1	6	4
24-VI-87	15%		0	3	2	2	0	7	1	3	5
21-II-88	5%		0	0	1	2	0	3	0	8	6
16-VI-88	20%		3	1	2	1	0	7	0	2	4
15-II-89	25%		0	0	0	0	0	0	1	1	2
14-IX-89	20%		4	2	4	3	2	15	2	4	6
26-II-90	20%		0	0	0	0	0	0	0	2	1
4-IV-90	10%		2	1	1	3	0	7	1	1	5
29-IX-90	25%		5	4	5	4	2	16	2	4	8
11-III-91	15%		0	0	0	0	0	0	0	1	2

leaf tissue along the edge, folding it over, and anchoring it with silk to the dorsal or upper leaf surface. As the larva grows, it abandons the smaller shelter and builds successively larger ones on the same and adjacent leaves. It is not uncommon to encounter many unoccupied but fully intact larval shelters on the food plant, as also noted for other Neotropical skippers exhibiting a similar behavior (e.g., Young 1991). In the smaller shelters, the larva rests on the ceiling formed by the flipped-over and tied leaf fragment. Larval body length expectedly appears correlated with length of tent shelters. An 11 mm long larva occupied a 19 mm long shelter; a 12–15 mm long larva was found in a 24 mm shelter, a 20 mm long larva in a 28 mm long shelter, and a 45 mm long (mature) larva was found in a 55 mm long shelter. Four mature larvae transported to Wisconsin gave an opportunity to observe tent-building behavior on prickly ash, *Zanthoxylum americanum* Mill. (Rutaceae), which they accepted and fed upon. Because mature prickly ash leaves are much smaller than mature *Citrus* leaves, shelter construction was different on the former food plant. Larvae confined in a plastic bag with prickly ash cuttings constructed shelters in the creases or folds of the bag, rather than in the leaves. In one instance a larva anchored two leaves in a cup-like configuration and used the flat surface of the bag as the rest of the shelter.

Larval abundance. Based upon several examinations of the *Citrus* bush between September 1985 and March 1991, it appears that larvae of *A. selva* are most abundant during the wetter times of the year, i.e., August–September, at this locality (Table 1). These periods correspond roughly with the highest incidents of new, flush leaves on the *Citrus* bush (Table 1). Even though high numbers of flush leaves occur at other times, such as a dry period in February, larval numbers are generally lowest at the drier times of the annual rainfall cycle at this site (Table 1). Such patterns are expected to vary considerably among different Costa Rican populations of *A. selva*, given the highly catholic geographical distribution of this skipper. Examination of specimens of *A. selva* in the Instituto Nacional de Biodiversidad (Inbio) collections in 1986 revealed diverse Costa Rican localities such as Escazu, Alajuela, Guanacaste, and Monteverde. The Allyn Museum of Entomology collection has specimens of *A. selva* from Limon Province, San José, and Santa Cruz in Costa Rica, in addition to specimens from El Salvador, Guatemala, and Mexico. Undoubtedly this widespread species occurs at many other localities in Costa Rica and Central America.

Various rutaceous larval food plants have been reported previously for *A. selva* and other species of this widespread Neotropical genus (Kendall 1965, Kendall & McGuire 1975, Biezanko et al. 1974). Larval food plants for this skipper in Costa Rica very likely include several species of *Xanthoxylum* in addition to cultivated *Citrus*. *Zanthoxylum* is a known food plant of *A. thraso tamenund* (Edwards) in southern Texas (Kendall 1965). *A. thraso* in Brazil has been recorded on *Citrus* and other Rutaceae (Moss 1949). The acceptance of prickly ash leaves by almost full-grown larvae of *A. selva* indicates its ability to feed on a temperate-zone *Zanthoxylum*.

Shelter building in *Achlyodes* larvae using their food plant leaves is well documented or noted in the literature (e.g., Moss 1949, Kendall & McGuire 1975). The precise function of such behavior, widespread and common among skippers, remains unknown. Both the larval and pupal stages of *A. selva* have been recorded as being parasitized (Kendall & McGuire 1975), suggesting that tent shelters of the larvae do not completely block parasitism. These shelters might be effective in concealing skipper larvae from insectivorous birds and lizards. It is unclear as to whether or not these shelters, which conceal or hide both larvae and pupae, reduce parasitism or other kinds of predation. In the present study, one larval shelter was packed with the 4 mm long cocoons, arranged in four rows of seventeen each, of an undetermined hymenopterous parasite, and a second one containing a row of six cocoons. The use of several different tent shelters in sequence by a larva, in which abandoned shelters are left intact, may reduce the effectiveness of searching behavior by predators or parasites, since time is lost checking unoccupied shelters for hosts or prey, as noted in another lepidopteran (Ruehlmann et al. 1988). Abandoned larval shelters of *A. selva* persist for many months, perhaps setting up a passive defense system by slowing down the rate with which predators or parasites locate larvae.

The occurrence of small larvae, and larval shelters, on the yellowish-green meristem leaves of *Citrus* in the present study suggests that *A. selva* females selectively oviposit on these leaves, and less so on darker green, mature leaves. Young leaves often have higher levels of water and nitrogen than older leaves on the same plant and larvae grow faster and achieve a higher body weight on meristem leaves (Pullin 1986). Population cycles of *A. selva* may be regulated to some extent by the annual cycle of peak production of flush leaves on its larval food plants. At least one Costa Rican butterfly species "anticipates" annual epics of peak meristem leaf availability by laying its eggs selectively on tiny leaf buds (Young 1983). Adults possibly mate near the end of the rainy season or early into the dry season, with gravid females entering into a phase of egg diapause until the rainy season commences. Mating pairs of *Achlyodes* sp. have been observed near Liberia, in Guanacaste Province, Costa Rica under shaded trees along the Pan-American Highway in the dry season (A. Young, S. Borkin, and J. Jass, pers. obs. Feb. 1984).

Kendall (1965) observed oviposition by *A. thraso tamenund* on *Zanthoxylum* in southern Texas but did not mention if eggs were placed on young or old leaves. *A. selva* probably oviposits on meristem leaves of its larval food plants, given the observation that young larvae, and their leaf shelters, occur most frequently on these leaves, and not on mature foliage. While females may prefer young leaves when available, oviposition may also occur on older leaves when meristem leaves are scarce or absent during the year. Empty egg shells of *A. selva* have been found on the older dark green leaves of *Citrus* in El Salvador (Stephen R. Steinhauser, pers. comm.). Both visual and chemical differences between meristem and older leaves (e.g., Saxena & Prabha 1975, Khattar & Saxena 1978) may guide females to oviposit chiefly on meristem leaves when they are available for rutaceous-feeding skippers, similar to what is known for swallowtail butterflies exploiting these plants (Vaidya 1969).

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VERIFICATION OF THE OCCURRENCE OF *LOTISMA TRIGONANA*
(COPROMORPHIDAE) IN ALASKA

Additional key words: British Columbia, Ericaceae, *Vaccinium*.

Lotisma trigonana (Walsingham) is thought to occur along the Pacific Coast of North America from Alaska to Costa Rica (Heppner 1986). The northern distribution of *L. trigonana* is based on abundant specimens from coastal Canada and one specimen from Alaska. Heppner (1986) reported 89 specimens of *L. trigonana* collected from 11 sites in British Columbia, Canada between 1899 and 1956, the most northern of which is Vancouver (49°15'N, 123°08'W). The existence of *L. trigonana* north of Vancouver is based on a single specimen labeled Orca, Alaska (60°39'N, 145°43'W), collected on the Harriman Alaska Expedition of 1899. Heppner speculated that Orca, as listed on the pinning label, may actually refer to the Orcas Islands of Puget Sound, Washington, where the Harriman Expedition may have started collecting specimens. Given the existence of only a single specimen in Alaska, and the possibility of a labeling error of that specimen, additional specimens from Alaska would greatly strengthen the conclusion that the range of *L. trigonana* extends through coastal Alaska.

We can verify the occurrence of *Lotisma trigonana* in and around Juneau, Alaska (58°18'N, 134°24'W). In August 1991, Gaither collected over 1000 berries of *Vaccinium* spp. (Ericaceae) from two locations along the Juneau road system. Many of these berries were infested with larval Lepidoptera. The berries were placed in plastic cups modified into rearing chambers. The cups had holes for drainage, a layer of sphagnum moss on the bottom, a wire mesh screen midway up the cup, and a nylon screen over the top of the cup. Berries rested on the wire mesh screen. In September and early October 1991 larvae emerged from the berries and entered pupation within the rearing cups. The pupae overwintered in the cups which were placed in outdoor covered cages. Over 100 adults emerged in April and May of 1992. De Benedictis examined adult specimens of both sexes and identified them as *Lotisma trigonana* (Walsingham).

The information presented here is the result of Gaither's dissertation research on the interactions between fruit-bearing plants and fruit-infesting insects. The research is ongoing and at present encompasses three summer field seasons. Future publications will present additional information on host plants and life history.

Voucher specimens are deposited in the Bohart Museum, Entomology Department, University of California, Davis, California. Roy A. Mask and Paul E. Hennon, both at Forest Health Management, Alaska Region, U.S.D.A. Forest Service, provided valuable advice and materials in our work. Mary F. Willson, Forestry Sciences Laboratory, U.S.D.A. Forest Service, provided generous logistic support.

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TEMPORAL CHANGES IN PRESENCE OF LATE INSTAR
MITOURA SPINETORUM (LYCAENIDAE) IN EASTERN OREGON

Additional key words: mistletoe, mimicry.

The thicket hairstreak, *Mitoura spinetorum* (Hewitson), feeds on several species of dwarf mistletoe plants, e.g. *Arceuthobium campylopodium* Englem. (Loranthaceae), which parasitize *Pinus ponderosa* Dougl. ex. Laws. (Pinaceae) (Shields 1965). Ballmer and Pratt (1992) proposed the genus *Loranthomitoura* to accommodate this species and four other North American hairstreak butterflies which utilize *Arceuthobium* as larval hosts, based on characteristics of immature stages, especially first instar chaetotaxy.

Mitoura spinetorum is distributed from Mexico to British Columbia (Shields 1965) and is recognized as a potential control agent for damaging mistletoe infections (Stevens & Hawksworth 1970). This insect produces at least two broods annually (Shields 1965, Pyle 1981), with adults flying from March to September in California and Oregon. Individual eggs are placed directly on the aerial shoots of the mistletoe plants, and the small yellowish olive larvae are well hidden amongst the masses of the host plant shoots.

We assessed the relative abundance and field periodicity of this species at Starkey Experimental Forest near Ukiah, Umatilla Co., Oregon, in 1992. In this area, ponderosa pine occurs mostly as small stands of open-grown trees, with branches extending nearly to the ground. Mistletoe plants were abundant on the lower branches of some trees, and numerous others could be seen on higher branches within the tree crowns.

In May 1992, three groups of 100 mistletoe plants each were marked with plastic flagging and numbered aluminum tags on the lower branches of selected ponderosa pines. To better represent the mistletoe plant population in an area, we marked only five plants per tree, each on a separate branch and usually on different sides of the host tree. Marked plant groups were separated by about 0.75 km.

At 8-10 day intervals through June and July, each mistletoe plant was carefully inspected to detect and record the presence of *M. spinetorum* larvae. Notes were kept on the location and developmental stage (relative size) of each larva found. Late-instar *M. spinetorum* are sluglike in shape and move slowly and infrequently; they often can be found feeding on the same or an adjacent mistletoe shoot for several days. Larvae in early stages are difficult to see under field conditions because mistletoe plants typically consist of dense clusters of aerial shoots and the *M. spinetorum* larval shape and coloration closely mimic the food plant (Remington 1958, Stevens & Hawksworth 1970, Ballmer & Pratt 1988). McCorkle (1962) states that the early instars of *M. johnsoni* Skinner feed by inserting their head into a hole chewed at the base of a scale on a mistletoe stalk. The cryptic and sedentary feeding habits of *M. spinetorum* apparently caused us to overlook younger larvae feeding deep in the masses of food plants. Accurate determination of all larvae present at any given time would require destructive sampling and careful dissection of the mistletoe plants. Because we did not want to destroy the marked mistletoe plants, most of the larvae we found were in the mid- to late-instars (usually 10-12 mm or longer) but, once recorded, could be relocated for a few days until they apparently were fully developed (approximately 18-20 mm long) and ready to pupate. Only a few of them persisted in larval form from one scheduled inspection time to the next.

No *M. spinetorum* larvae were found on marked plants until June 10, when two, each about 18 mm long, were located in plant group 2 (Table 1). Many others were recorded on June 18 and June 29, with the frequency peaking on June 29 and decreasing after that until none was present by July 27. Over the May-July period, a total of 11%, 19%, and 15% of marked mistletoe plants in groups 1, 2, and 3, respectively, were used by *M. spinetorum* larvae. The use of mistletoe plants on branches higher in the tree crown is unknown, but Remington (1958) quotes F. G. Hawksworth, who collected *M. spinetorum* larvae in Arizona, as stating that "Of about two dozen larvae taken, not one was found more than 10 feet above ground. However, relatively fewer of the host plants were examined in the higher parts of the pines, and it may be that *M. spinetorum* occasionally occurs much higher than any I found."

TABLE 1. *Mitoura spinetorum* larvae found on dwarf mistletoe at Starkey Experimental Forest in eastern Oregon, 1992.

Plant group	Number of larvae per 100 host plants by inspection date						
	1 June	10 June	18 June	29 June	7 July	15 July	27 July
1	0	0	3	11	3	3	0
2	0	2	4	14	2	4	0
3	0	0	8	4	4	1	0
Total	0	2	15	29	9	8	0

Most marked mistletoe plants hosted only one larvae, but eight of them had two each, one had four, and one had eight. In most cases, feeding damage to the host plant was not severe, except where the plant consisted of only a few aerial shoots or there were multiple larvae feeding on the plant.

Some larvae were collected for laboratory rearing to the adult stage; others were observed *in situ* until they disappeared, presumably to pupate. Comstock and Dammers (1938) and Tilden (1960) reported that pupation takes place in late July in the mass of food plant shoots. We were unable to locate any pupae in the field in spite of careful dissection of more than 30 large mistletoe plants. It may be that mature larvae drop to the ground and pupate in leaf litter under host trees.

From mature larvae brought into the laboratory for observation, two adult males were reared, one on June 30, the other on July 27, 1992. Both specimens are in the Pacific Northwest Research Station collection at Corvallis, Oregon.

From thirty-three other pupae held overwinter, no adults were reared. Parasites, identified as *Aprostocetus* sp. (Eulophidae) (Det. by Steve L. Heydon, Univ. California, Davis), emerged during February 1993 from all of them, usually 20–25 specimens from each pupa.

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DIFFERENCES IN SEASONAL PERFORMANCE OF TWENTY-SIX STRAINS OF SILKWORM, *BOMBYX MORI* (BOMBYCIDAE)

Additional key words: sericulture, cocoon yield, silk production.

Commercial exploitation of the mulberry silkworm (*Bombyx mori* L., Bombycidae) results in the production of 10,000 metric tons of raw silk in India annually (Thomas 1991). There are approximately 2000 different strains of *Bombyx mori* used in silk production (Reddy 1986). Twenty-one characters of this species are recognized as contributing to silk yield quantitatively or qualitatively (Chatterjee et al. 1990). These are: 1) fecundity; 2) hatching percentage; 3) missing percentage of young age larvae (i.e., early larval survival); 4) missing percentage of late age larvae (late larval survival); 5) total larval duration (i.e., rearing period); 6) fifth instar duration; 7) cocoon yield number per 10,000 larvae brushed [Silkworm eggs will be either on an egg sheet or in loose form. Brushing is the process of carefully separating the newly hatched larvae from the empty egg shells or egg sheets, and transferring them to the rearing trays with the help of a smooth brush.]; 8) cocoon yield (weight per 10,000 larvae brushed); 9) pupation rate; 10) single cocoon weight; 11) single shell weight; 12) shell ratio (i.e., ratio of single shell weight to single cocoon weight expressed in percentage); 13) mature larval body weight; 14) floss percentage [Floss is the foundation layer of the cocoon with entangled filaments from which a continuous silk filament cannot be obtained.]; 15) single cocoon filament length; 16) single cocoon filament weight; 17) filament size; 18) reelability percentage; 19) raw silk percentage; 20) neatness; and 21) boil-off ratio [Silk thread is reeled from the cocoons by boiling them in water so that the gummy materials are dissolved and the silk filament can be reeled without any breaks. The term is used in silk industry to classify the grade of raw silk with respect to reeling and weaving.]. While some of these characters are heritable, others are determined by environmental factors.

The domestic and international demand for silk always has been greater than can be met. In India, the average silk yield from indigenous strains of silkworms is around 30 kg/100 dfl (dfl = disease-free laying; one dfl equals approximately 500 eggs with an average 80% hatching, i.e., 400 worms). By contrast, in Japan the average yield is 60 kg/dfl. If the yield in India could be increased to 45 kg/dfl, overall silk production would increase by 50% (Thiagarajan et al. 1991). This may be achieved by rearing silkworm strains most suited for particular seasons. However, in India this practice is not employed. As a result, failures in rearings frequently lead to crop losses and frustration among farmers. To solve this problem and achieve maximal harvest, it is essential to select a few superior strains of silkworm in relation to seasonal performance. In Japan, there are 19 strains suitable for spring rearing (May-June) and 22 strains suitable for summer (July-August) and autumn (September-October) rearings (Shimizu & Tajima 1972). The purpose of our study was to evaluate the performance of different strains of silkworm available to us in relation to their performance in spring, summer, and autumn.

Materials and methods. Rearing experiments were conducted in the spring, summer, and autumn for three years (1989-1991) at the Regional Sericultural Research Station, Coonoor, in the Nilgiri Hills of Western Ghats, India. All of the twenty-six strains of silkworm available to us (Table 1) were reared in a randomized block design. Each group evaluated consisted of the larvae from a single laying by an individual female moth. All the larvae were retained until spinning. Each experimental tray was placed in a rearing stand; the positions of the trays were changed regularly three to four times a day to reduce effects of environmental factors. Standard techniques for rearing silkworms (i.e., temperature 23-28°C, relative humidity 79-90%, and 12/12 h dark/light ratio) were applied (Krishnaswami 1978). Duration of experimental rearings was 26 days for summer, 27 days for spring, and 28 days for autumn, with three replications of each strain.

Observations were made on five characters of economic importance: 1) cocoon yield (number per 10,000 larvae brushed); 2) single cocoon weight; 3) single shell weight; 4) shell ratio; and 5) filament length. Data were analyzed according to Lush (1954) and Kempthorne (1957).

TABLE 1. Salient characteristics of twenty-six silkworm strains used in the study.

Sl no.	Strain	Geographical origin	Larval marking	Cocoon color/cocoon shape/shell grains/floss amount
1	C108	China	Plain	White/oval/ordinary/less
2	C120	China	Plain	White/oval/medium/less
3	Dong306	China	Plain	White/short oval/medium/more
4	NN6D	China	Plain	White/oval, short oval/ordinary/less
5	J1 (M)	Japan	Marked	White/elongated constricted/ordinary/less
6	J2 (P)	Japan	Plain	White/elongated oval/medium/less
7	J2 (M)	Japan	Marked	White/deeply constricted/medium/less
8	JC2 (P)	Japan	Plain	White/oval/medium/less
9	CJ3 (P)	Japan	Plain	White/oval/medium/less
10	M2	Japan	Plain	White/slightly constricted/medium/less
11	SPC1	Japan	Plain	White/oval, short oval/medium/less
12	SPJ1	Japan	Marked	White/slender constricted/medium/less
13	SPJ2	Japan	Marked	White/slender constricted/medium/less
14	N4	Japan	Marked	White/constricted like dumbbell/medium/less
15	J122	Japan	Plain	White/oval, mildly constricted/medium/less
16	14M	Japan	Marked	White/dumbbell/medium/less
17	36 (PC)	Japan	Plain	White/dumbbell/medium/less
18	SN1*	Japan	Plain/marked	White/dumbbell/medium/less
19	NJ1*	Japan	Plain/marked	White/dumbbell/medium/less
20	JA1	India	Marked	White/dumbbell/medium/less
21	JB2	India	Marked	White/dumbbell/medium/fine/less
22	SH2	India	Plain	White/oval/fine/less
23	NB1	India	Plain	White/oval/medium/less
24	European	France	Plain	White/dumbbell/medium/less
25	JZH (PO)	Brazil	Plain	White/oval/medium/less
26	JZH (MC)	Brazil	Marked	White/constricted like dumbbell/medium/less

* Sex-limited strains. In a given strain, plain larvae are males and marked ones are females.

Analysis of variance of the five characters for twenty-six strains in three seasons and the strains/season interaction were evaluated as described by Pershad et al. (1986). A simple method for making a decision on each character based on least significant difference as described by Thiagarajan et al. (1993) was followed for each character for ranking of the races. The population means were arranged in groups based on *t*-test (and l.s.d.). The topmost group containing populations with the highest means was given a score 1, the next best a score of 2, and so on. If 'k' is the number of groups for a particular character, the populations in group 1 were given a score = $1/k$, those in group 2 a score = $2/k$, and so on to obtain standardized scores across the characters. The individual scores for each character were added up to provide a total score for each population. The populations then were ranked in descending order of the numerical values of total scores. The method consists of the following steps:

1. The performance of each character as demonstrated by its mean value in the particular entry or season and a score (actual score) is allotted to that character. A high mean value will get a score of 1; moderate value 2; low value 3 and so on.
2. The actual score assigned for a particular character is converted into a standard score by dividing actual score obtained with the number of scores applied. For example, in ERR character we used a total of 4 scores. Hence, the standard score will be "actual score/4."
3. A score or rank S_i is obtained for each entry [there are 4 entries in each race, which stand for (i) summer, (ii) spring, (iii) autumn and (iv) the average of three seasons] by multiplying standard score with the number of characters (which is 5 in this study).

$$S_i = s_{ij} \text{ (where } j = \text{number of characters)}$$

To demonstrate this method, here are the performance scores for 14 M in the spring season:

<u>Character</u>	<u>Actual score</u>	<u>Standard score</u>
ERR	1	1/4
Single cocoon weight	4	4/4
Single shell weight	1	1/4
Shell ratio	1	1/4
Filament length	4	4/4

Out of 5 characters, race 14 M received score 1 in 3 characters.

Results and discussion. The average rearing performance together with the least significant difference values of each character of the twenty-six strains of silkworm in spring, summer, and autumn seasons during three years is shown in Table 2. Analysis of variance, i.e., the mean squares for all the five characters, are given in Table 3.

Based on least significant difference values, the following strains are found to be most suitable to rear during particular seasons: European and 14 M (spring), JC2P (summer), M2 (autumn). These strains performed well for most of the characters of economic importance, especially cocoon yield. However, as illustrated in Table 2, the remaining strains also are useful for one or more characters.

The results of season specific performance of different strains with respect to characters like cocoon yield, single cocoon weight, single shell weight, shell ratio, and filament length noted in this study are in agreement with earlier reports on this subject (Venugopala Pillai 1979, Pershad et al. 1986, Thiagarajan et al. 1993). The results of the analysis of variance showed significant difference at the 1% level between the three seasons, twenty-six strains, and strains/seasons interaction for all the five characters studied. This indicates

TABLE 2. Mean values for five characters in twenty-six strains of silkworm in spring, summer and autumn seasons.

1 Sl no.	2 Strain	3 Season	4 Cocoon yield/ 10,000 larvae brushed (no.)	5 Single cocoon weight (g)	6 Single shell weight (g)	7 Shell ratio (%)	8 Filament length (m)
1	C108	Spring	8100	1.80	0.32	17.78	840
		Summer	9783*	1.78	0.25	14.05	821
		Autumn	8867	1.83	0.31	16.94	933
2	C120	Spring	8975	1.52	0.32	21.05*	935
		Summer	8500	1.47	0.28	19.05	929
		Autumn	7750	1.54	0.34	22.08*	1012
3	Dong306	Spring	9500*	1.68	0.26	15.48	889
		Summer	9700*	1.69	0.31	18.34	994
		Autumn	7900	1.06	0.23	21.70*	1042
4	NN6D	Spring	5861	1.45	0.27	18.62	976
		Summer	8417	1.67	0.28	16.77	845
		Autumn	9350*	1.62	0.28	17.28	940
5	J1 (M)	Spring	8475	1.62	0.31	19.14	928
		Summer	8567	1.74	0.33	18.97	1193*
		Autumn	9600*	1.60	0.32	20.00	987
6	J2 (P)	Spring	8475	1.70	0.37*	21.77*	1035
		Summer	8567	1.89	0.33	17.46	1018
		Autumn	9150	1.76	0.34	19.32	832
7	J2 (M)	Spring	8550	1.92	0.38*	19.79	1060
		Summer	9500*	1.78	0.30	16.85	890
		Autumn	9200	1.71	0.32	18.71	967
8	JC2 (P)	Spring	9475*	1.75	0.36	20.57	1077
		Summer	9217*	1.69	0.37*	21.89*	1192*
		Autumn	8550	2.01	0.42*	20.90*	1102
9	CJ3 (P)	Spring	8550	1.75	0.37*	21.14*	1194*
		Summer	9317*	1.77	0.34	19.21	1079
		Autumn	8388	2.13*	0.39*	18.31	1059
10	M2	Spring	9525*	1.45	0.29	20.00	1003
		Summer	9517*	1.66	0.33	19.88	1079
		Autumn	9750*	2.06*	0.43*	20.87*	1191*
11	SPC1	Spring	7950	0.50	0.30	20.00	1063
		Summer	8350	1.73	0.30	17.34	900
		Autumn	9250*	1.62	0.28	17.28	1102
12	SPJ1	Spring	9500*	1.65	0.30	18.18	1030
		Summer	8333	1.84	0.36	19.57	872
		Autumn	9000	1.63	0.31	19.02	1125
13	SPJ2	Spring	7275	1.70	0.30	17.65	963
		Summer	8400	1.72	0.35	20.35	928
		Autumn	9300*	1.63	0.37*	22.70*	1177
14	N4	Spring	6888	1.65	0.30	18.18	994
		Summer	6467	1.41	0.28	19.86	1067
		Autumn	5067	1.62	0.38*	23.46*	1229*
15	J122	Spring	9075	1.76	0.32	18.18	923
		Summer	8883	1.95	0.31	15.90	938
		Autumn	9550*	1.77	0.31	17.51	946

TABLE 2. Continued.

1 Sl no.	2 Strain	3 Season	4 Cocoon yield/ 10,000 larvae brushed (no.)	5 Single cocoon weight (g)	6 Single shell weight (g)	7 Shell ratio (%)	8 Filament length (m)
16	14M	Spring	9200*	1.75	0.40*	22.86*	1254*
		Summer	8900	1.84	0.38*	20.65	1044
		Autumn	8321	1.74	0.36	20.69	1147
17	36PC	Spring	8762	1.73	0.38*	21.97	1276*
		Summer	7567	1.86	0.35	18.81	1033
		Autumn	8433	2.05	0.37*	18.05	1039
18	SN1	Spring	6025	1.80	0.34	18.89	956
		Summer	8867	1.79	0.31	17.32	949
		Autumn	7917	1.68	0.35	20.83	1242*
19	NJ1	Spring	5825	1.83	0.37	20.22	11.07
		Summer	8917	1.86	0.37	19.89	1170
		Autumn	8450	2.05	0.41	20.00	1240*
20	JA1	Spring	4425	1.67	0.35	20.10	1202*
		Summer	9633*	1.67	0.32	19.16	1128
		Autumn	8700	2.04	0.41*	20.10	1111
21	JB2	Spring	9565*	1.78	0.32	17.98	1007
		Summer	8383	2.12*	0.40*	18.87	1175
		Autumn	8347	1.97	0.41*	20.81	1164
22	SH2	Spring	7150	1.68	0.36	21.43*	1285
		Summer	7517	1.85	0.38	20.54	1271
		Autumn	6505	2.09*	0.40*	19.14	1101
23	NB1	Spring	9575*	1.75	0.33	18.86	1023
		Summer	9633*	1.90	0.31	16.32	838
		Autumn	9450*	1.67	0.30	17.96	967
24	European	Spring	9240*	1.86	0.39*	20.97*	1187*
		Summer	9167	1.75	0.31	17.71	1064
		Autumn	8600	1.96	0.39*	19.90	1075
25	JZH (PO)	Spring	9100	1.62	0.30	18.52	1151
		Summer	9517*	1.76	0.30	17.05	993
		Autumn	7650	2.16*	0.39	18.06	1087
26	JZH (MC)	Spring	9200*	1.70	0.29	17.06	863
		Summer	8450	1.99	0.38*	19.10	1059
		Autumn	8150	1.99	0.38*	19.10	1129
LSD at 5% level			583	0.10	0.06	2.62	101

* Significant at 5% level.

that not only heredity but also environmental factors influence the performance of a given strain for the characters studied.

In addition to the leaf quality of mulberry in different seasons, physical factors such as temperature and relative humidity (RH) also greatly influence the growth of silkworms (Gabriel & Rapusas 1976). First and second instars reared at 26–28°C temperature and 80–90% RH are healthier in later stages (third, fourth and fifth instars). Temperature, RH, and ventilation during the spinning of silkworms influence the quality of cocoon. The length of silk filament also may vary in the given strain in different seasons (Ueda et al. 1969). Recent experiments have shown that physical properties such as cocoon

TABLE 3. Mean squares for five characters in *Bombyx mori* L.

Source of variation	df	Cocoon yield	Single cocoon weight	Single shell weight	Shell ratio	Filament length
Seasons	2	534,050* F = 4.63	0.288** F = 12.00	0.011** F = 11.00	38.71** F = 15.42	8780** F = 7.80
Strains	25	548,104** F = 4.76	0.144** F = 6.00	0.009** F = 9.00	14.14** F = 5.59	8505** F = 7.55
Strains × seasons	50	570,470** F = 4.95	0.161** F = 6.71	0.008** F = 8.00	30.28** F = 12.06	7971** F = 7.08
Error	206	115,231	0.024	0.001	2.51	1126

* and ** Significant at 5% and 1% level, respectively. df = degrees of freedom.

weight, shell weight, and filament length will be optimal when mature *Bombyx mori* are kept at 21–24°C temperature and 67% RH.

Since domestication of silkworm, mankind has been interested in breeding silkworm varieties that produce greater quantities of silk. Silkworm breeders in sericulturally advanced countries like Japan and South Korea have always utilized season specific silkworm strains. Mano et al. (1991) recommended the hybrid N147 × C145, with high cocoon shell weight and long filament length, as a suitable silkworm race for the spring season. Similarly, Sohn et al. (1990) have produced a hybrid silkworm variety named Samkwang-jam suitable for summer and autumn rearings with high silk yielding ability.

To obtain the best cocoon crop quantitatively and qualitatively, a particular strain should be reared during the season in which the environmental conditions are most favorable for its genotype. Knowing that variation caused by the environment can be produced in the offspring by repeating the environmental treatments, which produced them in the parent, we can exploit successfully the cocoon crops from 14 M and European in spring, JC2P in summer, and M2 in autumn seasons.

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BOOK REVIEWS

BUTTERFLIES IN THAILAND, VOL. I (PAPILIONIDAE AND DANAIDAE), Third Revised Edition, by Brother Amnuay Pinratana and John N. Eliot (photographs by A. Pinratana and text by J. N. Eliot; check lists by Y. Kimura). 1992. Distributed by Bro. Amnuay Pinratana, St. Gabriel's College, Bangkok 10300, Thailand. 174 pp., map, check lists, 92 color plates. Hard cover, 19 × 27 cm, no ISBN. \$43.00 U.S. (postpaid).

This is a newly updated and thoroughly revised third edition, co-authored by the eminent authority John N. Eliot, of Volume I of the six-volume series on Thailand's butterfly fauna, published between 1977 and 1988. Virtually all the problems I had with the original volume, in terms of organization, illustration, and identification, have been eliminated in this revision and I found the text extremely useful and valuable to any student of southeast Asian Lepidoptera. Particularly valuable is the inclusion of a map of Thailand, although its usefulness would be greater had the provinces been delineated rather than just identifying major towns and cities, because the collecting data in the text refers to provincial locations. The charts of collecting data, listing dates of collection and location for each species, are particularly helpful since many Thai butterflies are localized in distribution and fly only in specific seasons. Perhaps the greatest improvement in this edition is the exceptional clarity and color of the illustrations which show, in most cases, both males and females and dorsal and ventral views, when applicable. The text, which was extremely brief in the earlier editions, is even more concise in this revision but this is offset by the excellent photographs, which preclude the necessity of extensive written descriptions. The pertinent details of each species—physical descriptions (both male and female), wingspan, distribution, and remarks as appropriate—follow the original format, although references such as "rare," "very rare," etc., have been dropped. The terminology for body and wing venation illustrations have also been omitted.

A valuable new feature is that each photograph is labeled with the Latin name of the species rather than with a number as in the earlier editions, which required extensive searching of the book to locate the appropriate descriptive text. Subsequent revisions would benefit if each photo caption indicated as well on what page the species entry is to be found, as the photographs and written material now appear in different parts of the book. Finding the species descriptions is difficult because the list of scientific names appears on page 75, in the middle of the book, and the check lists for both Papilionidae (page 3) and Danaidae (page 51) do not indicate on what page of the book the text is located. This might best be compiled into one expanded table of contents, now located on page 80, to appear at the front or back of the book for easier reference. In the first edition the text appeared opposite the illustrations, obviating this need, but in this revision the text and illustrations occupy separate sections of the book.

Having collected personally for some eight years in virtually all parts of Thailand, particularly the Peninsular area, leaves me astounded with the wealth of new species that are constantly coming to light. Pinratana has added numerous new records to the text for species that formerly were unknown to occur in Thailand or for which only very fragmentary information existed. I note that the female form *esper*i of *Papilio memnon agenor*, illustrated in earlier versions, was dropped in the new edition with no evidence of collecting data. The vague reference in earlier editions to its existence in Yala Province of the Thai Peninsula did not reappear in the new text. I have collected this form in Pattani Province, adjacent to Yala, and thus can confirm its occurrence in Thailand. A peculiarity of distribution in Thailand exists for *Papilio paris* to which no particular reference is made in the book. It is common throughout northern Thailand and a collection record is indicated for Prachuab Province north of the Isthmus of Kra. It then disappears entirely, according to present knowledge, from the Thai Peninsula and throughout West Malaysia only to reappear in Java and Sumatra.

The text follows current taxonomic revisions made by Ackery and Vane-Wright on the Danaidae and by Hancock, Igarashi, and Miller on the Papilionidae. Without questioning the validity of these reclassifications, I confess that the current papilionid classification is

a bit confusing (depending on whether the reader is a splitter or lumpers by inclination) because all *Atrophaneura*, variously known as *Polydorus*, *Byas*, *Panosomia*, *Tros* or *Balignina*, have now been lumped into two genera: *Parides* and *Pachliopta*. Photographic captions of the *Papilionidae*, when the genus is identified only by "P.", cannot be easily interpreted; without referring to the text, it is difficult to differentiate *Papilio*, *Parides*, or *Pachliopta*. Subgeneric names are now given for many species; *Graphium*, for example, now includes subgenera *Pathysa* and *Pazela*. Many well known southeast Asian species have been reclassified: *Euploea d. diocletianus* is now *E. r. radamanthus*, *Idea jasoni* (sp. *Iasonia*) *logani* is now *I. stollis logani*, *Chilasa mahadeva* is now *Papilio* (subgenus *Principis*) *mahadeva*, several species of former genus *Danaus* have been reassigned to new genera such as *Paranthica* and *Tirumala*, and the former *D. vulgaris* and *D. similis* are now included in *Ideopsis* (subgenus *Radena*). Although probably quite justified from a taxonomic standpoint, it takes a bit of mental refocusing to bring the relationships back to an understandable level.

The book is well bound with a high quality cover with gilded lettering and a dust jacket with a photo of *Teinopalpus imperialis*, one of Thailand's recent and rarer additions to its insect fauna. The photographs are on glossy paper and provide excellent detail. The book has been well proofed to eliminate errors and spellings and what few I noticed were already listed on an errata sheet. All in all, this third revision is an exceptionally nice book that is a worthwhile addition to any collection. It contains much up-dated and revised information about the butterflies of Thailand and adjoining geographical areas that has not appeared before in print. I can only hope that with time similar revisions will appear for the other five volumes in the series.

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KEYS TO THE JAPANESE BUTTERFLIES IN NATURAL COLOR, by Toshio Inomata. 1990. Hokuryukan, 3-21 Kanda Nishiki-cho, Chiyoda-ku, Tokyo 101, Japan. In Japanese. 64 + 224 pp., 402 text figs., 103 color plates. Gold stamped hard cover with transparent wrap, slipcased; 15.5 × 21.5 cm, no ISBN, 4800 Yen (about \$39.00 U.S.).

As the title suggests, this book provides keys to all of Japan's 256 recorded butterfly species from the order level to the subspecies level, and it does so quite thoroughly.

The book starts with a short foreword by Yoshihiko Kurosawa, former executive of the Zoology Department at the Japanese National Science Museum, a brief introduction, and a lengthy table of contents. A brief discussion of the phylogenetic placement of the order Lepidoptera within the kingdom Animalia, instructions on how to use the book's dichotomous keys, and a brief description of important anatomical features used in the keys follow. The next section contains keys to family, subfamily, tribe (for Papilionidae and Lycaenidae), and genus for all Japanese butterflies. This 49 page dichotomous key first identifies all of the world's butterfly families, elaborates upon Japan's eight butterfly families, and organizes them by subfamily. Each subfamily is split into genera, and each generic description is accompanied by a sepia tone photograph of a Japanese member of that genus. Each generic description includes the number of the plate where the species and subspecies of that genus are fully illustrated. Throughout the keys, figures showing important taxonomic features are provided. For example, photographs or line drawings of hesperiid legs are shown in all instances where they are taxonomically significant. Drawings of wing venation are presented throughout the keys, showing differences in wing venation at family, subfamily, and generic levels. The last 224 pages of the book (which are numbered separately from the first 64 pages) consist of 103 two-page color plates, an Index that lists all the Japanese butterflies in Japanese, an Index that lists each

species by scientific name, and a short Bibliography. The only mistake that I noticed among the few sections printed in Latin letters is the incorrect spelling of W. H. Howe's surname (as "How") in the bibliography.

The most impressive aspect of this book is the quality and number of color plates. Each two-page color plate consists of at least one full page of pictured specimens on the right page. The facing page contains at least one full map of Japan showing in colored outlines the distribution of each butterfly species and subspecies treated on that page. Detailed discussions of each species' and subspecies' distribution, biology, foodplants, and variations, and a separate color plate that shows rare or stray species with additional variations of the species pictured on the adjacent page, are provided in almost all plates. This smaller "color plate within the color plate" is also frequently used to explain and illustrate in more detail differences between similar species. The plates are separated by family, and then by genus. A dichotomous key to the species in each genus is provided at the beginning of each generic treatment, and is always highlighted in boxes with a pastel colored background for immediate visual access. Additional tawny colored boxes provide more detailed information on several species, such as their taxonomic history or seasonal variation. Citations of taxonomic revisions are often given in the tawny boxes. Species names are written in both Japanese characters and Latin letters. Colored blocks on the edge of each plate, which can be seen even when the book is closed, show the location of each family within the plates.

The color plates are the finest I have ever seen in a book on butterflies. They are equal to or better than the plates in the MONA series. Every specimen shown is in fresh condition, except for two stray specimens with small imperfections. Full specimens are usually shown, and wing borders are cut off at the edges of plates only on larger specimens. Each color plate contains 7 to 32 specimens, shown against a light gray-blue background. Shadows are very slight and never draw attention away from the butterflies. Even white Pierids are excellently illustrated, which is very difficult in plates photographed against pale backgrounds. The completeness of the color plates is impressive. For example, 28 specimens of *Lycaeides subsolanus* Eversmann are illustrated on page 111, showing every slight variation on both the dorsal and ventral surfaces. The comprehensiveness of the color plates is indicated by the fact that 1967 specimens are pictured, and only 256 species of butterflies are known from Japan! The quality of the plates is eloquent testimony to the expertise of the Japanese in color printing, and the overall design of the book is superlative!

Inomata is to be congratulated on the impressive thoroughness and beauty of his book, which must be seen to be fully appreciated. Although written in Japanese, at a fairly technical level, the value of this book even to lepidopterists who are not fluent in Japanese cannot be understated. Even if you have little interest in the butterflies of Japan, this book is well worth \$39.00, just for the color plates. I recommend this book to any person with interest in Palaearctic or Holarctic butterfly fauna.

ANDREW D. WARREN, *Department of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853*. [The assistance of Toko Morimoto in accurately reading the Japanese is gratefully acknowledged, and the comments on this review provided by Robert Dirig are sincerely appreciated.]

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FLORISSANT BUTTERFLIES: A GUIDE TO THE FOSSIL AND PRESENT-DAY SPECIES OF CENTRAL COLORADO, by Thomas C. Emmel, Marc C. Minno, and Boyce A. Drummond. 1992. Stanford University Press, Stanford, California 94305. Hardcover (ISBN 0-8047-1938-1), \$35.00; Softcover (ISBN 0-8047-2018-5) \$14.95; 21 × 28.5 cm, 148 pp., 9 color plates, 58 halftones, 1 map.

This small book is a unique mixture of information about the fossil butterflies and present-day butterfly fauna of the Florissant Valley region of central Colorado. The authors report on the status of fossil butterflies and the results of a sporadic long-term survey of the region's living butterflies.

The book is basically an annotated, illustrated list of the fossil butterflies and the living butterflies of the Florissant Valley. The Florissant Fossil Beds is one of the most important fossil insect deposits in the world, but the living butterfly fauna is relatively poor in comparison to other areas of Colorado.

The discussion of the fossil butterflies is brief and might better have appeared as an appendix. Its value is that all Florissant fossil butterflies are illustrated and discussed in the same place. For the first time in any butterfly book, the butterfly fossils are assigned common names and are also listed in a separate checklist.

There are 19 pages of introductory material that describe the ecology of the Florissant area and give background information on habitats, behavior, reproduction, and other aspects of the region's butterflies. There is a list of pertinent references and a glossary at the end of the text.

The bulk of the book is comprised of species accounts of the butterflies now known from the Florissant Valley. There are numerous excellent black and white photographs scattered through the text (it's a pity that they couldn't have been in color) and nine excellent color plates of specimens and a few photos of living butterflies. The illustrations seem to be properly identified in almost all cases, but a specimen of *Phyciodes tharos* is identified as *Phyciodes pallidus*, a butterfly that apparently does not occur in the study area. To clarify "tharos-group" relationships in the book, the butterfly referred to as *Phyciodes tharos pascoensis* should be more properly referred to as *Phyciodes selenis*, as it is not consistent to have two subspecies of the same species occupying the same small area.

I would have liked more detail on the occurrence of the butterflies in the study area, and a comparison between the Florissant butterfly fauna and that of a few other well-studied Colorado areas along the Colorado Front Range.

I recommend this book as an addition to the library of any lepidopterist interested in the Rocky Mountain butterfly fauna. The prospective reader will find it to contain excellent background material for the Colorado fauna. Even though the book covers only a small geographic area, it will be useful for most montane habitats along the Colorado Front Range. Any lepidopterist who has taken or plans to take field courses about butterfly biology at the Nature Place in Florissant will find it invaluable.

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BUTTERFLIES OF THE BULOLO-WAU VALLEY, by Michael Parsons. 1992. Wau Ecology Institute Handbook No. 12. Bishop Museum Press, P.O. Box 19000-A, Honolulu, Hawaii 96817. 280 pp., 23 text figs., 22 color + 3 b/w plates. Softcover, 12.5 × 23 cm, ISBN 0-930897-61-7. \$34.95 (+ \$2.00 p&h).

In the 1980's Michael Parsons was the butterfly ecologist working for the Papua New Guinea (PNG) Insect Farming and Trading Agency (IFTA). His enthusiasm and commitment helped to establish an ideal and successful integration of the utilization and conservation of the butterfly resource in PNG with studies of the taxonomy, distribution, behavior and ecology of Papuan butterflies. The need for IFTA to develop butterfly farming (technically "ranching"!) in out-of-the-way areas of the country provided opportunities to investigate the faunas of remote parts of PNG. The collecting of butterflies

by villagers for the commercial side of IFTA's activities provided distributional data unusual for a Third World country.

This book covers an area of PNG, the Bulolo-Wau Valley, which is only about 350 km² in extent, although it includes the well-known Mt. Kaindi (2388 m) and other mountains. Remarkably, 373 species of butterflies and skippers have been recorded from the area. The author points out that this represents about half of the species known to inhabit the whole of PNG, including the Islands. The area also includes the IFTA headquarters, the Bulolo Forestry Institute and, of course, the Wau Ecology Institute.

The book is well organized, with a map of the Bulolo-Wau Valley and another showing the Melanesian Region and major sub-regions. The author has crammed a great deal of useful information into his Introduction, and has struck a good balance between giving help to the beginner and inexperienced, and providing up-to-date scientific information for the specialist. It is good to see the Comstock-Needham scheme of venation preferred to the esoteric and old-fashioned numerical system still favored by some lepidopterists. The narrow pages of the book have very wide margins (more than a third of the width of the page) but this does allow for the inclusion of some text figures. Those of resting attitudes of representatives of the families are particularly helpful, and indicate that the author is an expert field lepidopterist.

The main part of the book is an account of each species recorded from the Bulolo-Wau Valley. There are helpful aids, such as diagrams of wing-pattern and genitalia drawings, for distinguishing closely related species. The size range of both sexes of each species is given, essential in a book in which the figures of butterflies have been, disconcertingly, reproduced to a standard size. The information provided for each species is excellent and thoroughly up-to-date, but it demonstrates how much work still remains to be done on the fauna of even this part of New Guinea. There is a short and rather selective glossary, a list of food plants, a good bibliography, and a comprehensive index.

It is perhaps captious to mention any omission in a text so full of sound and interesting information. However, I would have liked to see a short section on the relationships between local people and the butterflies of the region—what one might call ethno-lepidopterology. Certainly in some parts of PNG there is local knowledge of butterflies, including their larvae ("sneks" in pidgin), while birdwings (*Ornithoptera priamus* in most cases) are used for personal adornment. Perhaps, however, this does not occur in the Bulolo-Wau Valley.

This is a book which will be indispensable to anyone studying the butterflies and skippers of New Guinea. Unlike many more lavish and expensive texts, it is based on intimate knowledge of the species in the field. The comments on status and behavior are therefore particularly authoritative and valuable. Moreover, the excellent balance among utilization, conservation, and science is a notable feature. I hope this book will stimulate more work on these three interrelated aspects of butterflies, not only in the Bulolo-Wau Valley, or even PNG, but more widely in southeast Asia.

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INSECTS OF PANAMA AND MESOAMERICA: SELECTED STUDIES, by Diomedes Quintero and Annette Aiello (editors). 1992. Oxford University Press, 200 Madison Avenue, New York, New York 10016. 720 pp., 1268 illustrations. Hardcover, 23 × 28 cm, ISBN 0-19-854-018-3. \$195.00.

The slender and sinuous shape of the Isthmus of Panama belies its biological importance, which stems from the tenuous and geologically recent link it provides between North

and South America. For nearly three million years the Isthmus has provided a continuous land corridor between the continents, resulting in the mixing of their faunas, and has served as a center for speciation and biological diversification. Not surprisingly then, Mesoamerica (the region from southern Mexico to Colombia), with the Isthmus as its crooked spine, boasts one of the highest diversities of insect species in the world.

In a remarkable series of beautifully illustrated volumes published between 1879 and 1915, F. D. Godman and O. Salvin compiled the first comprehensive inventory of this rich fauna in *Biologia Centrali-Americana*. During the intervening century, the rate of tropical forest destruction in Mesoamerica and elsewhere has accelerated relentlessly. Today, the Pacific lowland forests of Panama have been virtually extirpated, along with many of the species originally described in *Biologia Centrali-Americana*, and other forests in the region are threatened. Thus, it was with a sense of great urgency that the work reviewed here was prepared. *Insects of Panama and Mesoamerica: Selected Studies* was written with the hope of stimulating more interest in this biologically rich region by assembling and publishing as much information as possible about the insects of these endangered Central American forests.

The result is a large and impressive volume comprising many different kinds of studies, of varied duration, and conducted at a broad assortment of sites within the region. Written for students and interested general readers as well as for entomologists, this book has 42 chapters written by 52 biologists from 11 countries. This diversity of coverage is both its strength and weakness. The contributors offer a wide variety of viewpoints, writing about behavioral ecology, morphology, systematics, taxonomy, ecological diversity, and biology, but the coverage of the different insect groups is wildly uneven. Of the 30 insect orders (including Collembola; the book follows the arrangement in N. P. Kristensen, 1981, *Phylogeny of insect orders*, *Ann. Rev. Entomol.* 26:135-157), only 21 are included: 13 are dealt with fairly completely, or at least include a checklist to species for the area covered in the chapter, and 8 are treated incompletely, with focus on only one or a few groups; 9 are not covered at all.

The book is well organized and beautifully produced, in keeping with the excellent series of publications on natural history to come from Oxford University Press during the past several years. To provide an evolutionary context, there are two introductory chapters: "Geological Setting and Tectonic History of Mesoamerica" and "Biogeography of the Panamanian Region, from an Insect Perspective." [No, the author of the latter chapter does not have six legs!] The remaining 40 chapters are grouped by Order, proceeding phylogenetically from Collembola to Diptera. The text is augmented by more than 1260 line drawings, distribution maps, and black and white photographs, in addition to numerous data tables, dichotomous keys, and species checklists. Reference sections at the end of the book include a set of abstracts in English and in Spanish (resúmenes), a taxonomic index, and a subject index.

Of interest to lepidopterists are the five chapters in the Lepidoptera section. These are an eclectic mix: three chapters concern butterflies that act like butterflies, one chapter treats butterflies that act like moths, and the remaining chapter deals with moths that act like butterflies. A better introduction to the deceptive complexities of tropical Lepidoptera could hardly be found. Let's start with the butterflies that behave as they are supposed to, all of which happen to be in the Nymphalidae.

Many of the most familiar Central American butterflies are members of the Nymphalinae (Nymphalidae), for which Gerardo Lamas M. and the late Gordon B. Small, Jr., present an annotated list of the Panamanian species. Their chapter on this subfamily includes notes on distribution, type locality, depositories of type material, synonyms commonly encountered in frequently used literature, and references to published illustrations. A chapter by Annette Aiello explores the ecology of two members of the Nymphalidae in some detail, contrasting their different responses to a severe dry season: *Anartia fatima* (Nymphalinae) contracts its range and persists only in wet Atlantic forest refugia, whereas *Pierella luna luna* (Satyriinae) appears to survive the dryness in pupal diapause. Such contrasting life history strategies contribute to the ecological and behavioral diversity of butterfly communities, adding yet another layer of complexity to the already bewildering taxonomic diversity that characterizes tropical forests. The third chapter on Nym-

phalidae, by Julian Monge-Najera, is a guide to the clicking butterflies (*Hamadryas*) of Panama, and includes a checklist and descriptions of species, an illustrated key to their identification, and a discussion of their biology and behavior, with emphasis on sound production.

In a chapter profusely illustrated by photographs, drawings, charts, and graphs, Neal G. Smith has assembled a wealth of natural history information on *Urania fulgens* (Uraniidae) (the moth that acts like a butterfly). Smith's comprehensive chapter discusses this diurnal moth's ecology, reproductive behavior, developmental biology, and migration in great detail, contrasting its Central American and Panamanian populations with what is known of the Cuban species, *U. boisduvali*.

Finally, we get to the butterfly that acts like a moth. Veterans of the tropics are familiar with the crepuscular habits of species in the genera *Brassolis*, *Dynastor*, *Opisphanes*, and *Caligo* (all Nymphalidae: Morphinae), which rest during the day and night and become active only for a short period at dawn and dusk. Other than these creatures of the twilight and a few Satyrinae with similar behaviors, all other butterflies are active only during the day, right? Wrong, says Annette Aiello, who describes the nocturnal habits of little-known family Hedyliidae, previously thought to be moths in the family Geometridae and only recently recognized as butterflies, a conclusion based primarily on morphological and behavioral characters of the immature stages (see M. J. Scoble, 1986, Entomol. Scand. 21:121–158). Aiello lists nine species of Hedyliidae reported from Panama, providing brief descriptions of wing color and pattern and references to published photographs of adults. Most importantly, she presents previously unpublished details of the life history and larval behavior of *Macrosoma semiermis* (Hedyliidae), a common Panamanian "nocturnal butterfly."

Lepidopterists will be hard put to justify spending almost \$200 to purchase a book that devotes less than 7% of its 700 pages to butterflies and moths, but entomologists in general and tropical ecologists in particular will find this valuable compendium a bargain in spite of the price. Certainly, this volume should be on the shelves of all research libraries so that it is readily available to those with an interest in the ecology and conservation of that fragile and priceless treasure—the tropical rainforest.

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BUTTERFLIES OF THE FLORIDA KEYS, by Marc C. Minno and Thomas C. Emmel. 1993. A Mariposa Press Edition by Scientific Publishers, P.O. Box 15718, Gainesville, Florida 32604. 168 pp., 29 color plates, 52 color figures and line drawings. Hardcover (ISBN 0-945417-88-8; \$31.50) or Softcover (ISBN 0-945417-87-X; \$18.95), 22 × 28.5 cm. Order from publisher (add \$2 postage per copy; \$3.50 outside USA.)

Butterflies of the Florida Keys is more than just another "Butterflies of . . ." It is a well written and beautifully illustrated natural history guide, bursting with butterfly trivia. The main body of the text, a 103-page section/chapter appropriately entitled Butterflies of the Florida Keys, is preceded by a 32-page introductory chapter. The Introduction includes numerous maps, graphs, and beautiful color photographs accompanying sections on Climate, Historical Perspective, Vegetation and Plant Communities, The Keys Butterfly Community, Conservation, Precautions, and Note on Species Accounts. All of the graphs are crisp and clear and most of the photographs have been reproduced beautifully. This portion of the text is in an easy reading style and nicely subdivided into the major sections listed above. A detailed table on butterfly monthly occurrence, descriptions (and photographs) of plant communities, a brief review of Caribbean bioge-

ography, and a summary of conservation efforts in the Florida Keys all contribute to the completeness of the introductory material.

The main body of the text details the 106 species of butterflies and skippers recorded from the Keys. At the beginning of each family, there is a brief summary of the morphological, biological, and behavioral features that characterize that family. Each species account consists of five subheadings: Description, Distribution, Natural History, Flowers Visited, and Status. Both common and Latin names are provided, and all taxa are considered at the subspecific level. In addition to the full color plates illustrating spread specimens of all of the species (including upper and under surface, males and females where necessary), there are photographs of larvae and pupae of select exemplars of each family in their natural habitats. Most of the color plates are crisp and clear, and all are shadow-free. However, some are a bit too dark and two of the plates of the Pieridae are a little fuzzy. [What kind of a review would this be if I didn't find *something* to criticize?]

In addition to the standard data provided in the species accounts, for some of the more "interesting" species there is considerably more information. For example, the species account for the monarch (*Danaus plexippus*) is augmented by a map of North America illustrating the major migration routes of this species. The species account for the barred sulphur (*Eurema daira*) includes two half-page black and white photographs illustrating the seasonal forms and sexual dimorphism exhibited by this highly variable species.

Butterflies of the Florida Keys may find a spot on your coffee table, in your research library, or in your suitcase if you have the opportunity to visit the Keys. It is an outstanding and thorough faunal (butterfly) survey of a unique place in North America.

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BUTTERFLIES OF BAJA CALIFORNIA: FAUNAL SURVEY, NATURAL HISTORY, CONSERVATION BIOLOGY, by John W. Brown, Herman G. Real, and David K. Faulkner. 1992. The Lepidoptera Research Foundation, Inc., 9620 Heather Road, Beverly Hills, California 90210. v + 129 pp., 9 text figs., 8 color plates, 155 species distribution maps. Softcover, 21.3 × 27.5 cm, ISBN 9611464-4-3. \$25.00.

Baja California is a land of fascinating mystery and intriguing natural history. It is hard to believe that the first butterfly from Baja California was reported as early as 1875, by no less authority than Samuel Scudder (mentioning *Vanessa carye* from Isla Guadalupe off the western coast of Baja California). Just eight years later, Henry Edwards described the first endemic subspecies (now called *Phoebis agarithe fisheri*) from near La Paz. And in that same year, William Greenwood Wright published a brief description of a field trip listing 23 species taken along the northwestern coast of the peninsula. Since those early studies, many authorities have visited Baja California and collected there, involving at times some very adventurous expeditions.

Now, three noted modern lepidopterists have combined forces to publish this exciting new treatment of the whole butterfly fauna of the Mexican states of Baja California Norte and Baja California Sur. John Brown and David Faulkner of the Entomology Department of the San Diego Natural History Museum worked on a preliminary manuscript assembled by Herman Real, who had earlier done a Master's thesis on the Pieridae of Baja California. Together, these three authors gathered thousands of records from museums and private collections across the United States and abroad. Many unpublished notes were provided by those who had the most experience with collecting various butterfly groups in Baja California. The product is this truly impressive and biologically important book.

After a brief introduction to the purpose of the book, the authors trace the fascinating history of the pursuit of butterflies up and down Baja California, including names and dates of every known significant collecting expedition (through 1990). This historical section is followed by a detailed description of each of the phytogeographic regions in these two Mexican states. The authors include diagrams of average monthly temperature and average monthly precipitation for six representative sites distributed across Baja California. The description of each biological province includes representative plants, geographical and geological notes, and typical annual changes in the climate.

The peninsula of Baja California, one of the longest (1300 km) yet narrow "linear" peninsulas in the world, is an excellent natural laboratory for the study of peninsular biogeography. The authors review three models that have been proposed for the origin of the peninsular fauna in general, and then present a scenario for the origin of the butterfly fauna itself. Although the peninsula probably was separated from the west coast of mainland Mexico about 15 million years ago, there is also evidence that the opening of the gulf may have not begun until about 5.5 million years ago. Further evidence suggests that elevated sea levels once submerged much of what is now the peninsula, leaving the higher regions exposed as large islands. Some of these areas may have served as refugia from which many species later spread northward. The impacts of these geological changes on the peninsular fauna have indeed been manifold.

Following this general discussion of biogeography is a short but detailed section on endemism in Baja California, from which 21 butterfly taxa have been described. The introductory material concludes with two short sections on butterfly phenology and conservation biology, in which the effects of human development on this sparsely populated peninsula are reviewed, together with their apparent impact on butterfly populations.

The bulk of the book is devoted to a systematic account of all species of butterflies (178) for which the authors were able to personally examine specimens known to be from Baja California. A separate section of unverified records includes 25 species. Nomenclature throughout follows that of the Hodges (1983) checklist. Common names, when used, were taken from either Opler and Krizek (1984) or Emmel and Emmel (1973) or Pyle (1981). Each species account starts with the scientific name, author, and common name, followed by a citation of the color plate and figure number illustrating the species. A brief synonymy includes only the original description and references that actually cite that species' occurrence in Baja California. The abbreviated citations here are amplified in the extensive Literature Cited section at the end of the book. A subsection on Peninsular Distribution includes the type locality for each taxon described from Baja California, and detailed habitat and geographical notes on the locations, including islands, where it occurs in this Mexican region. The following section, Flight Period, gives the months that the butterfly flies in each section of Baja California, along with notes on the number of broods. This is followed by a section on Larval Hosts, including published and unpublished citations for each record. Most species accounts then include a Remarks section, which presents interesting facts about the species' distribution or absence from certain places, the taxonomic status of the species or subspecies, or other notes. Finally, many accounts end with a section on Specimens Examined, which includes detailed localities and dates for each unusual record (or all capture records if the species is known from less than 25 specimens or fewer than 5 collecting localities).

Accompanying each species' description is a map of the peninsula with distributional records indicated as black dots. The topographic features are sufficient to locate each of these localities in coordination with the "Specimens Examined" list of records. The book's text concludes with a thorough Literature Cited section, in which all references dealing with butterflies from Baja California are listed in full. Eight crisp, clear color plates showing specimens at almost life-size accompany the text. These color plates illustrate at least one specimen of every species from the peninsular fauna. Where sexual dimorphism occurs, or ventral color pattern elements are important in the identification, two to four specimens of such species are shown to illustrate these differences. The color reproduction is excellent and accurate. The only slightly distracting feature is the presence of shadows cast between specimens by the lighting arrangement used. (This reviewer understands

that the foreign printer was to have used computer masking to eliminate shadows, and that both the publisher and authors were surprised at this result.)

Every lepidopterist interested in the faunas of southwestern North America and the neotropics will want to buy a copy of this inexpensive and beautifully produced book. Its comprehensive, indeed exhaustive, treatment of all the significant collections of Baja California material, and the outstanding combination of authoritative authorship and editorial care by the publisher, guarantee that this work will remain the standard reference on the butterfly fauna of Baja California for many decades to come. The work will also be of interest to those who study the biogeography and evolutionary history of butterflies. Baja California, because of its isolation and relatively well-known geological history, offers insights that are widely applicable and of interest to the worldwide community of lepidopterists. I recommend this book enthusiastically.

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BUTTERFLIES AND SKIPPERS OF OHIO, by David C. Iftner, John A. Shuey, and John V. Calhoun. 1992. Bulletin of the Ohio Biological Survey, New Series, Volume 9, Number 1. The Ohio Lepidopterists Research Report No. 3. College of Biological Sciences, The Ohio State University, Columbus, Ohio 43210. 212 pp., 40 color plates. Softcover, 21.5 × 28 cm, ISBN 0-86727-107-8, \$40.00 (plus \$5 p & h). Order from Ohio Biological Survey, 1315 Kinnear Road, Columbus, Ohio 43212-1192.

This well-designed book (the cover painting and design are by John V. Calhoun) consists primarily of 144 species accounts arranged according to family. It is an unusually thorough text and could well be used as a model for future regional or state books of butterflies and skippers. The book is dedicated to Ohio lepidopterists, who likely will supply the bulk of the sales; however, this is an excellent reference volume for every lepidopterist.

Butterflies and Skippers of Ohio begins with a foreword by Paul A. Opler of the United States Department of the Interior Fish and Wildlife Service. A subsequent preface by the authors tells the reader that one of the major goals of the book was to make this publication as complete as possible so that it could be used as a foundation for the study of Ohio lepidoptera. In this they have certainly succeeded.

The introductory section is completed with a brief introduction and a section on the history of butterfly study in Ohio, accompanied by the names and photographs of some of the more significant researchers and collectors (the massive butterfly net of Homer F. Price surely must have cast fear into the hearts of butterflies within his reach!). All joking aside, this is an interesting, historically worthwhile section, and something that is lacking in most regional books about butterflies and moths.

The authors then provide us with an overview of previous research on Ohio's butterflies and skippers, a section on education and conservation (well-done, but too short), and an overview of the ecological and historical factors that influence the distribution of species in Ohio. These sections are well done and highly readable, in particular the section concerning the ecological parameters of Ohio's butterflies. Here they discuss the geological setting of Ohio, the influence of the glacial periods, the physiographic regions of Ohio, the botanical communities of Ohio (forest types, prairies, wetlands, and modified habitats), and postglacial biogeography.

A subsequent methods section details the sources and handling of data presented, and describes the format used in the species accounts. A checklist of species reported from Ohio completes the introductory material.

The species accounts section is introduced with a state map that records the number of species from each Ohio county, followed by a species richness map based on the number of resident species recorded from each county. Each individual account lists the species' residential status, as well as its distribution/range, habitat, and larval hostplants. Adult energy resources and flight periods are also given. Following each species identification is a list of similar species (the authors identify diagnostic characters that separate look-alike species), and general comments (including observations concerning behavior, phenotypic variability, and aberrations). A distribution map and a histogram (if there are enough data) that details the seasonal flight period are also included—the latter alone should be extremely useful to all lepidopterists in the state. Each species account ends with a listing of unverified county records.

The text concludes with a discussion of species that may occur in Ohio (even though they have not yet been recorded), and a section about species that have been erroneously reported from the state. There is a brief (but very usable) glossary of terms that may be unfamiliar to amateur lepidopterists, and a sound bibliography with over 300 entries that provides full references to literature cited in the text and that serves as general reference. Following the glossary and bibliography are an appendix that lists regional lepidopterological societies and an appendix that lists the abbreviation codes for Ohio counties as used in the plate captions. There are also an index to reported Ohio hostplants, an index to common names of butterflies and skippers, and an index to taxa of butterflies and skippers.

The 40 color plates which conclude the book illustrate the natural vegetation of Ohio (Plate 1), a geographic and cross section of Ohio (Plate 2), and photographs of typical habitats that support uncommon to rare lepidopterans (Plates 3–6). Plate 7 is an excellent composite photographic summary of butterfly behaviors (including basking behaviors), and Plates 8–40 illustrate Ohio's butterflies and skippers (the species here are represented in phylogenetic order, which approximates the order of the species accounts in the text—a useful feature for cross-referencing). For most species, ventral and dorsal figures of both sexes are illustrated. In total, over 600 specimens are figured.

I agree with Paul Opler, who found this text to be one of the most accurate, thorough, and complete treatments of a state's butterfly fauna yet published—the result of 10 years of cooperation among the Ohio Lepidopterists, the Ohio Biological Survey, and the Ohio Department of Natural Resources, Division of Wildlife. It far exceeds the caliber of similar state guides. This book will be a valuable reference and a useful field (and research) resource for professional and amateur lepidopterists, conservationists, wildlife managers, and all those who are generally interested in the wildlife of Ohio. I also believe this book will set a new standard for regional (Lepidoptera) texts and I applaud the authors for taking such a bold new approach.

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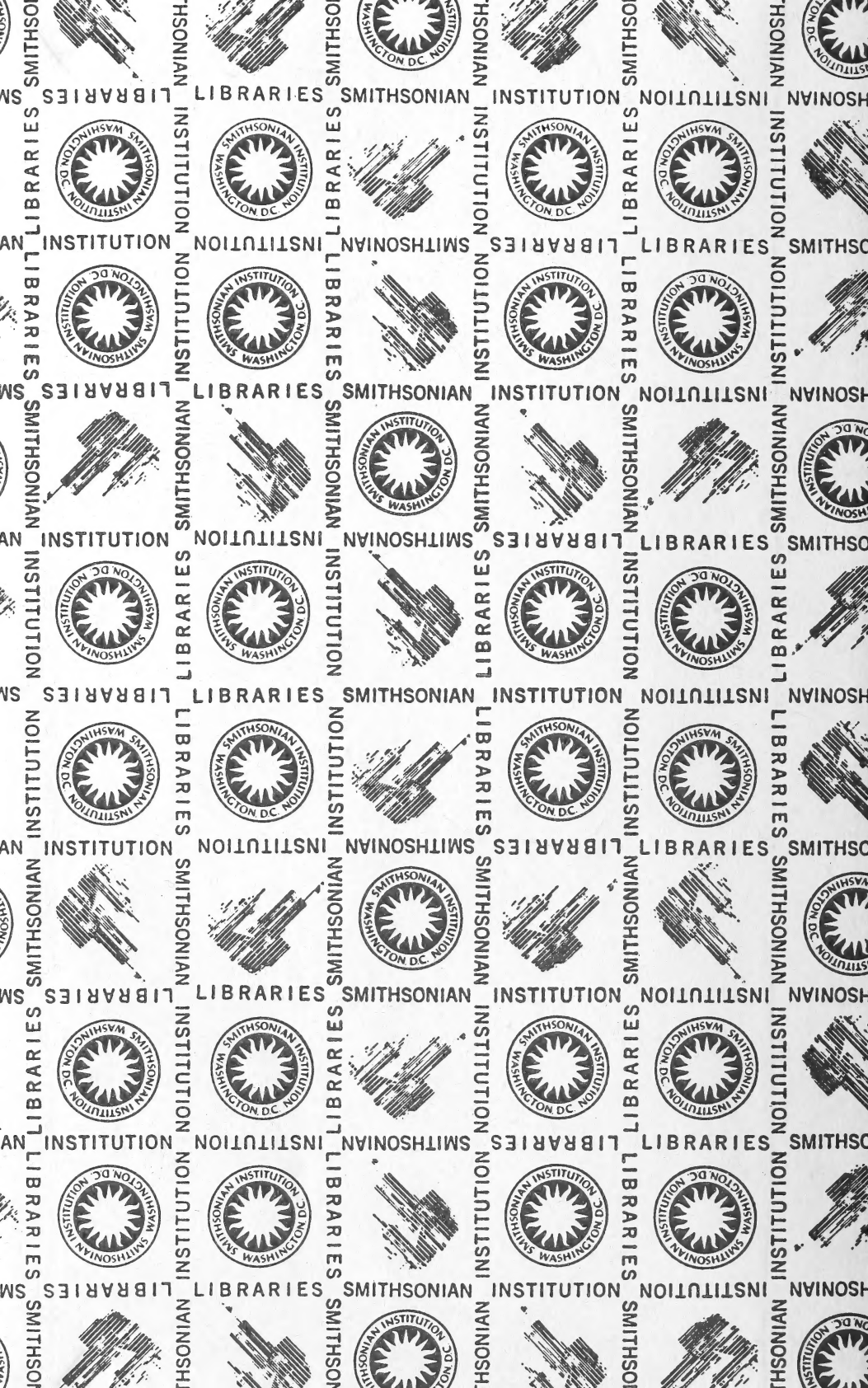
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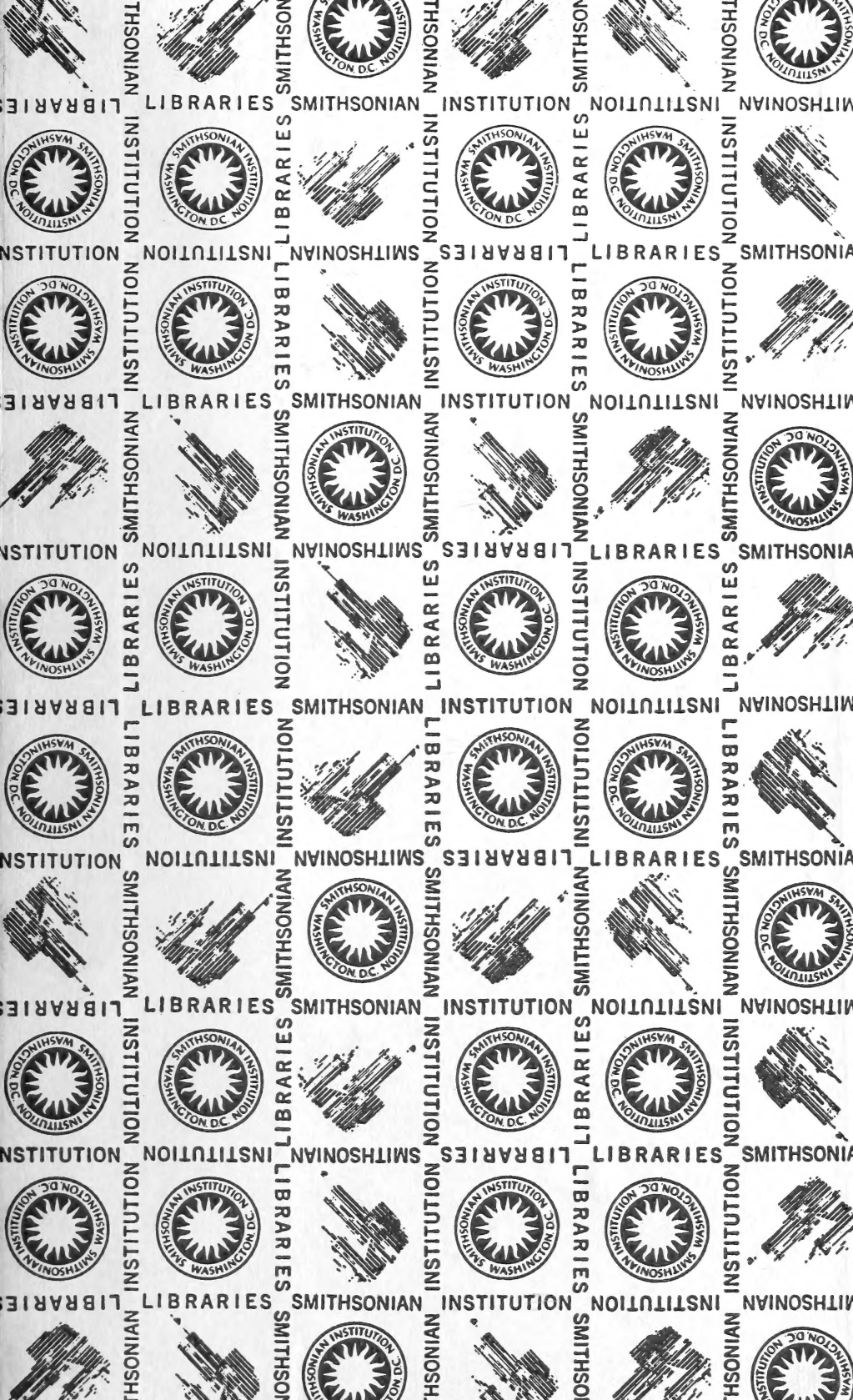
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